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POPULATION DENSITY OF NORTHERN SPOTTED OWLS IN MANAGED YOUNG-GROWTH FORESTS IN COASTAL NORTHERN CALIFORNIA

LOWELL V. DILLER

Simpson Timber Company, P.O. Box 68, Korb, CA 95550 U.S.A.

DARRIN M. THOME

U.S. Fish and Wildlife Service, 2321 West Royal Palm Road, Suite 103, Phoenix, AZ 85021 U.S.A.

ABSTRACT.—We estimated population densities of Northern Spotted Owls (*Strix occidentalis caurina*) in managed young-growth forests in coastal northern California from 1991–97. The 1266 km² study area was divided into three subregions (Klamath—666 km², Korb—392 km² and Mad River—208 km²) and completely surveyed each of the seven years. A total of 446 individual owls was marked to generate both empirical and Jolly-Seber (J-S) estimates of density. Mean empirical and J-S estimates of abundance were similar but mean estimates of crude density (territorial owls/km²) differed among the three subregions (Klamath— 0.092 ± 0.006 [\pm SE], Korb— 0.351 ± 0.011 , Mad River— 0.313 ± 0.017 and overall mean— 0.209 ± 0.009). Significant differences in forest age-class composition among the three subregions provided a plausible explanation for the low Klamath density but did not account for the similar densities observed in Korb and Mad River. Ecological densities (number of individuals/area of habitat) were higher than crude densities but the interpretation of this was limited because only nesting habitat was used to estimate suitable habitat. Compared to limited published reports, densities were relatively high in two of the three subregions in our study but this was probably typical of Northern Spotted Owl densities for portions of coastal northern California. Recognizing the limitations of using density to indicate habitat quality, our study provided valuable baseline data for assessing long-term trends in Northern Spotted Owl population dynamics within the study area.

KEY WORDS: *Northern Spotted Owl*; *Strix occidentalis caurina*; *California*; *density*; *managed forests*; *mark-recapture*.

Densidad poblacional de *Strix Occidentalis caurina* en los bosques jóvenes y manejados de las costas del norte de California

RESUMEN.—Estimamos la densidad poblacional de *Strix occidentalis caurina* en bosques jóvenes y manejados de las costas del norte de California entre 1991–97. Los 1266 km² del área de estudio fueron divididos en tres subregiones (Klamath—666 km², Korb—392 km² y Mad River—208 km²) y los monitoreamos durante los siete años. Un total de 446 individuos de buhos fueron marcados con el fin de generar estimativos de densidad empíricos y de Jolly-Seber (J-S). La media empírica y los estimativos de J-S de abundancia fueron similares, pero la media de densidad cruda (buhos territoriales/km²) difirió en las tres subregiones (Klamath— 0.092 ± 0.006 [\pm SE], Korb— 0.351 ± 0.011 , Mad River— 0.313 ± 0.017 y la media promedio— 0.209 ± 0.009). Las diferencias significativas en la edad y clase de la composición de los bosques entre las tres subregiones pueden ser la explicación de la baja densidad de Klamath pero no para las densidades similares observadas en Korb y Mad River. Las densidades ecológicas (número de individuos/área de habitat) fueron mayores que las densidades crudas. La interpretación de esta fue limitada debido a que se utiliza el habitat de anidación para estimar habitats convenientes. Al comparar la limitada publicación de reportes, se encontró que las densidades fueron

relativamente altas en dos de las tres subregiones de nuestro estudio. Quizas esto sea típico de las densidades de *Strix occidentalis caurina* en porciones costeras del norte de California. Al reconocer las limitaciones de usar densidades para indicar la calidad de habitat, nuestro estudio provee valiosos datos para evaluar tendencias en el largo plazo sobre la dinámica poblacional de *Strix occidentalis caurina* dentro del área de estudio.

[Traducción de César Márquez]

The Northern Spotted Owl (*Strix occidentalis caurina*) is associated with mature and old-growth forests throughout much of its range. This relationship has been studied primarily through radio-telemetry data that infers habitat selection through disproportionate use of mature- and old-growth forests relative to their occurrence within a landscape (Forsman et al. 1984, Carey et al. 1990, Solis and Gutiérrez 1990, Carey et al. 1992). In addition, studies of Northern Spotted Owl occurrence and abundance have shown a greater number of owl sites in mature- and old-growth forests relative to adjacent young forests (Forsman et al. 1977, Forsman et al. 1987, Forsman 1988, Bart and Forsman 1992, Blakesley et al. 1992). Given the economic value of mature- and old-growth forests, the association of Northern Spotted Owls with these forests places it at the center of a major controversy in the Pacific Northwest. The 1990 listing of the Northern Spotted Owl under the federal Endangered Species Act (USDI 1992) instituted management policies limiting timber harvest of Northern Spotted Owl habitat on public and private lands (Thomas et al. 1990, Gutiérrez et al. 1996, Marcot and Thomas 1997).

The population density of a species is important to resource managers for several reasons. In harvested game species, it is important to increase population density to generate a greater harvestable surplus, and it may also be important to understand the population density relative to carrying capacity (Krebs 1985, Caughley and Sinclair 1994). In species of conservation concern, population density has been used as one of the indicators of habitat quality (Forsman 1988, Thomas et al. 1990, Bart and Forsman 1992), and one of the criteria for establishing federally designated critical habitat areas (USDI 1992). In many populations, density has been used as a surrogate for knowing vital rates of populations that allow estimation of the population stability or viability.

Most attempts to compare abundance of Northern Spotted Owls in different habitats have relied on estimates of relative abundance (Forsman et al. 1977, Marcot and Gardetto 1980), because esti-

mating population density has been difficult for a species that exists in low numbers and occupies large home ranges. As a result, reliable estimates were not possible unless large areas were surveyed (Franklin et al. 1990).

We surveyed 1266 km² of managed young-growth forests for seven years as part of a monitoring plan for the Northern Spotted Owl under Simpson Timber Company's (STC) Habitat Conservation Plan (Simpson Timber Company 1992). The primary objective of this study was to estimate population density of owls in three subregions with different forest age-class compositions to provide baseline data for assessing long-term trends in Northern Spotted Owl populations within a managed young-growth landscape. We compared crude (number of individuals/total area, Odum 1971) and ecological densities (number of individuals/area of habitat; Odum 1971), and assessed changes in owl density during the study period (1991–97). In addition, we compared estimates of abundance based on empirical (direct counts of individuals for which differences in detectability and sampling variation associated with the estimate are not known) and mark-recapture methods. Comparability of these two approaches, empirical versus mark-recapture, is important since most of the reported estimates of Spotted Owl population density are based on abundance estimates derived from empirical data.

STUDY AREA

The study area was primarily within 1558 km² of land owned by STC located in Del Norte, Humboldt and Trinity counties, northwestern California. Most of this property lies within 32 km of the coast, but can extend up to 85 km inland. The study area was located within the Northern California Coast Range physiographic province where fog is common (Mayer 1988). Near the coast, mean summer and winter temperatures are about 18°C and 5°C, respectively, whereas extremes of 38°C in summer and –1°C in winter are not uncommon beyond the longitudinal belt of coastal influence approximately 48 km from the coast. Precipitation ranges from 102–254 cm annually, with 90% of this falling from October–April (Elford 1974).

Predominate forest stands in the study area were coastal redwood (*Sequoia sempervirens*), Douglas-fir (*Pseudotsuga*

menziesii), and oak woodlands (Zinke 1988). Species characterizing the oak woodlands included tanoak (*Lithocarpus densiflorus*), California black oak (*Quercus kelloggii*) and Oregon white oak (*Q. garryana*). Many of the redwood and Douglas-fir stands also contained a large component of the following hardwoods: tanoak, bigleaf maple (*Acer macrophyllum*), madrone (*Arbutus menziesii*), California bay (*Umbellularia californica*), and red alder (*Alnus rubra*).

Since the late 1960s, the primary silvicultural practice has been even-aged management involving relatively small clearcuts (12–24 ha in size) followed by prompt replanting. About 97% of the study area consisted of young forests ranging from 0–80 yr old. Residual trees (left from past logging operations) were a component of some forest stands and commonly the largest, oldest trees present.

METHODS

Within STC lands, Northern Spotted Owl survey boundaries were established *a-priori* based on ownership patterns, topographic features, vehicular access and other logistic considerations. The resulting study area was further subdivided due to geographic and vegetative patterns. In a nearby study area, Franklin et al. (1990) determined that areas exceeding 90–130 km² were sufficient to accurately estimate Northern Spotted Owl density. Three subregions in our study area met this criterion and hereafter are referred to as Klamath (666 km²), Korbel (392 km²) and Mad River (208 km²; Fig. 1). Other isolated tracts of STC property were too small to be included as separate subregions. Following Thome et al. (1999), we created six categories of stand age to classify habitat: 0–5, 6–20, 21–40, 41–60, 61–80, and >80 yr (Table 1). The 61–80 and >80 yr age classes were combined for this analysis, because there was very little area of one or both of these age classes in the three subregions.

We surveyed the entire STC study area for Northern Spotted Owls at least twice each season using a complete and systematic search protocol from 1 March–30 August, 1991–97. Prior to initiation of surveys, we inspected the entire study area using 1:24 000 aerial photographs. We plotted call points at strategic locations that maximized observer ability to solicit and detect responses from owls. Call points were usually positioned at relatively high elevations with unobstructed forest openings to ensure a clear and far-ranging broadcast of the call. Solicitations consisted of playing recorded Northern Spotted Owl calls or vocalizing imitations of calls for a minimum duration of 10 min. We used a jet boat to access and survey STC property bordering the Klamath River. All surveys using this protocol were conducted nocturnally, beginning no earlier than dusk. If an owl responded to a nocturnal call, its location was plotted, and a daytime follow up effort was initiated, where an observer attempted to locate the roosting owl by pursuing responses made to imitated or recorded calls (Forsman 1983). We captured owls using noose or snare poles (Forsman 1983) and banded them with a USGS band on one leg and a plastic, color-coded band on the other (serving as a unique identifying mark; Forsman et al. 1996). Sex and age were determined following Forsman (1981, 1983) and Moen et al. (1991).

We calculated forest stand ages using STC's timber inventory database in Intergraph's CAD system, integrated with the Modular Graphics Environment 5.0 (Intergraph Corporation 1994) geographic information system (GIS). Forest stands were distinguished based on date of harvest and polygons were drawn around unique forest stands. Only GIS data from 1997 were available for analysis. Landscape data from 1997 were considered adequate because the mean annual percent change in the landscape (from timber harvest) during this study was 0.7 ± 0.08 [\pm SE], 1.0 ± 0.18 and $0.5 \pm 0.16\%$ for the Klamath, Korbel and Mad River study areas, respectively.

Not all of the land surveyed was owned by STC, because other private lands (in-holdings) were common within our study area, and survey boundaries were set by topographic features and access points rather than ownership boundaries. Since GIS coverage was limited to STC lands, we were able to assess age-class conditions for 90% (599 km²) of Klamath, 75% (294 km²) of Korbel and 70% (145 km²) of Mad River. Despite this, we believe the GIS coverage was representative of the entire study area, since most of the landscape was subjected to the same historic timber harvesting practices that created entire watersheds with similar aged stands. In addition, the in-holdings and adjacent lands associated with the Korbel and Mad River subregions (areas with the least GIS coverage) were virtually all private lands zoned for timber production. We compared the amount of forest in the five age classes among the three subregions (Table 2) using Chi-square analysis (Hintze 1997).

We used the Jolly-Seber (J-S) capture-recapture model (Jolly 1965, Seber 1965, 1982) that allowed for death and immigration in open populations. We used program JOLLY (Pollock et al. 1990) to calculate J-S estimates of annual abundance (N_t). Because population and density estimates on STC lands had never been documented, we were primarily interested in these parameters from the modeling. We subjectively chose the reduced parameter J-S model (model D in program JOLLY) to analyze the data, because reduced parameter models compute abundance estimates with greater precision than models saturated with parameters (Jolly 1982). Ninety-five percent confidence intervals were calculated as 1.96 (SE [N_t]). Goodness-of-fit tests (Pollock et al. 1985) in program JOLLY were used to determine if the models fit the data. When goodness-of-fit tests suggested lack of fit, we used a variance inflation factor, \hat{c} , based on quasi-likelihood theory (Burnham et al. 1987:243–246, McCullagh and Nelder 1989) to adjust variances in models with overdispersed data (Lebreton et al. 1992, Anderson et al. 1994). The variance inflation factor is calculated as χ^2/v where χ^2 was the goodness-of-fit statistic with v degrees of freedom. Expected values for \hat{c} are not, on average, different from 1.0 with models that fit the data, and do not exceed ≈ 4 in models that attain structural adequacy, but may need variance inflation measures (values of 6–10 indicate complete model inadequacy requiring an entirely new model). If \hat{c} indicated that variance inflation measures were necessary, the standard error of each population parameter was calculated as $\sqrt{\hat{c}}\{SE\}$ (Anderson et al. 1994).

Empirical estimates of annual abundance (N_t) followed criteria established in Franklin et al. (1990), which

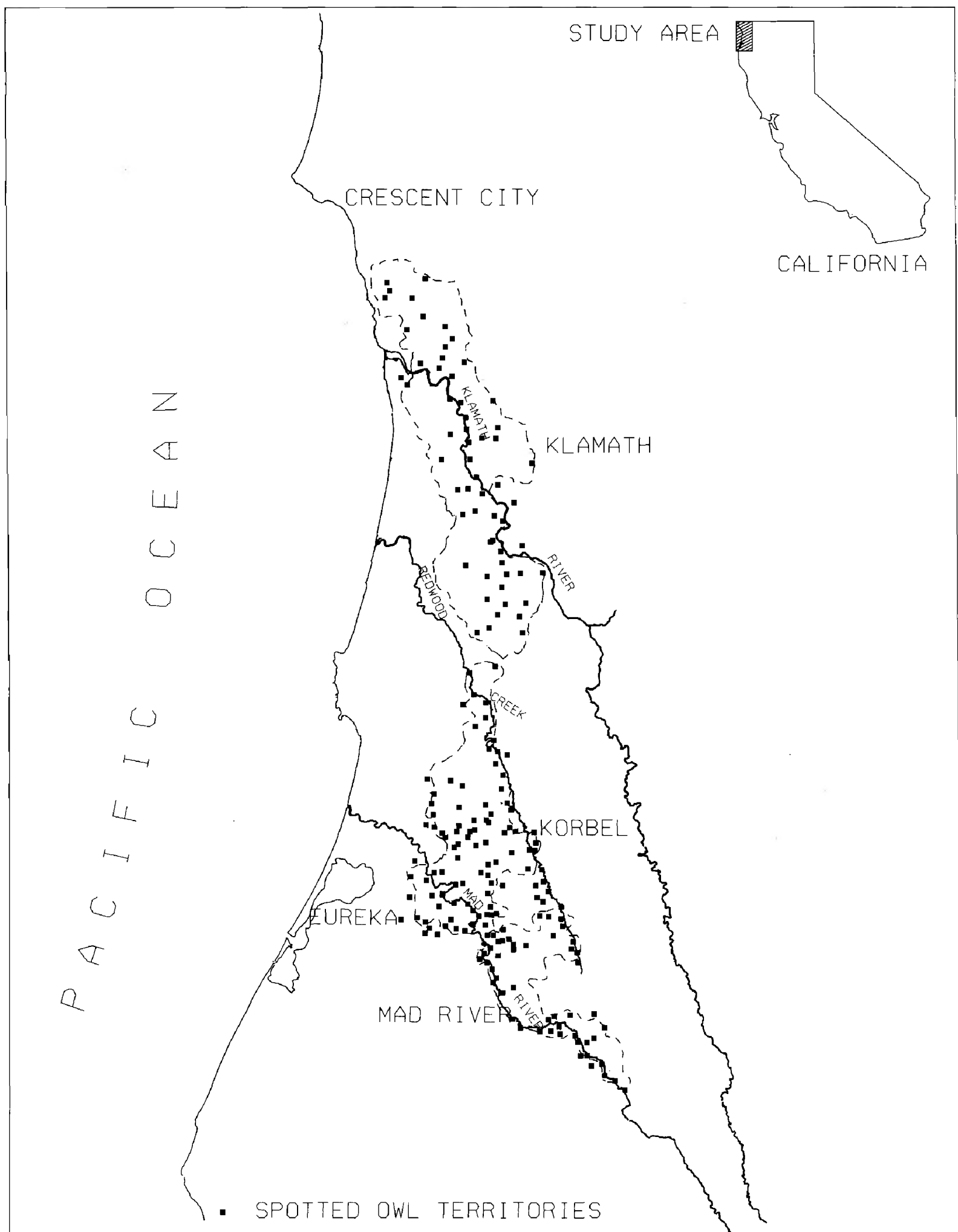


Figure 1. Map of the Simpson Timber Company study area, northwest California. Dots represent Northern Spotted Owl locations within and adjacent to Klamath, Korbels and Mad River subregion boundaries.

Table 1. Description of six forest age categories used in analysis of Northern Spotted Owl ecological density for the Simpson Timber Company study area in northern California, 1991–97.

AGE CATEGORY	TREES/ha		BASAL AREA ^a		VOLUME ^b	
	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD
0–5	0.9	5.9	0.2	1.0	0.1	0.7
6–20	42.2	160.8	2.3	8.4	0.8	4.3
21–40	558.6	292.6	29.7	15.8	6.7	7.4
41–60	708.2	320.9	46.9	18.5	14.6	11.2
61–80	591.4	384.9	59.1	18.3	29.8	19.8
>80	811.6	598.9	58.4	30.7	28.7	27.8

^a m²/ha.
^b Million board m/ha.

assumed an annual census of territorial owls in which all individuals known to be alive in the study area were counted. The total annual count was based on surveys over the 7-yr period and included the: number of identified (banded) individuals; number of unidentified individuals mated to identified owls; and number of unidentified individuals assumed different from identified individuals in nearby territories.

Population density was estimated as crude density (N_t /total area; Odum 1971) and ecological density (N_t /area of habitat; Odum 1971). We used J-S estimates of adult and subadult Northern Spotted Owls within the three subregions for N_t . Following the rationale of Franklin et al. (1990), we used the estimated total quantity of Northern Spotted Owl habitat as the divisor to calculate ecological densities. In their study, the proportion of telemetry locations of owls in different habitats was used as one method to estimate total owl habitat. Old-growth, which had the highest proportion of telemetry locations, was assigned a weight of 1.0 with other habitats weighted based on the proportion of telemetry locations in those habitats relative to those in old-growth (Franklin et al. 1990). Since we had no telemetry data to assess foraging habitat in our study area, we calculated the total owl habitat in each subregion based on the relative amount of nesting habitat.

To calculate ecological densities, we assigned a weight of 1.0 for the >60 yr age class, because it had the highest proportion of nest sites relative to the total forested area in the age class (0.27 nests/km²). Other age classes were

then weighted (normalized) by dividing the proportion of nest sites in those age classes by the proportion of nests in the >60 yr old age class (Table 3). For example, there were 0.18 nests/km² in the 41–60 yr age class, which was 68.5% of the density found in the >60 yr old age class. Crude densities were calculated as N_t (J-S) divided by the size of the associated subregion. Ninety-five percent confidence intervals for the density estimates were calculated by dividing the population confidence intervals by the subregion size (Seber 1982).

Abundance estimates cannot be computed for the initial year of study using program JOLLY. Therefore, we used preliminary capture data from 1990 as the first year of analyses, even though a complete census protocol was not established until 1991 (Franklin et al. 1990). In 1990, we banded and subsequently entered in the analysis, 14, 76 and 17 owls from Klamath, Korbøl, and Mad River, respectively. We used program CONTRAST (Hines and Sauer 1989) to examine differences in abundance estimates among years for the three subregions. Program CONTRAST uses a general Chi-square statistic to test differences among abundance estimates using contrasts (Sauer and Williams 1989). We first tested for overall homogeneity in abundance estimates for each subregion. If a test yielded significant results, we then tested *a-posteriori* to determine which years were causing heterogeneity. Alpha levels for *a-posteriori* tests were adjusted to maintain the overall experiment-wise error rate (Neter and Wasserman 1974). We used the Bonferroni approach of using α/m as the significance level for unplanned compar-

Table 2. Percent of forest habitat in five age classes and percent of nonforest on three subregions of the Simpson Timber Company (STC) study area in northern California.

SUBREGION	FOREST AGE CLASS IN YEARS					NONFOREST	NONSTC ^a
	0–5	6–20	21–40	41–60	>61		
Klamath	4.3	27.9	49.4	5.2	10.6	2.6	10.0
Korbøl	6.0	24.8	31.2	24.3	10.1	3.5	25.0
Mad River	3.6	3.8	16.0	23.8	34.2	18.6	30.0

^a Percent of total study area within each subregion that was not within STC ownership or for which there was no forest age class information.

Table 3. Habitat weight and amount of weighted habitat in each age class for three subregions of the Simpson Timber Company study area in northern California. Habitat weights were calculated from 86 nest sites of Northern Spotted Owls, 1991–97.

	FOREST AGE CLASS IN YEARS					TOTAL ^a
	0–5	6–20	21–40	41–60	>61	
Habitat weight ^b	0	0.02	0.20	0.68	1.00	
Amount of weighted habitat ^c by subregion (km ²)						
Klamath	0	2.8	66.4	23.8	70.8	163.7
Korbel	0	1.4	24.7	65.3	39.6	131.1
Mad River	0	0.1	6.7	33.9	71.1	111.9

^a Excludes nonforested areas.
^b See methods for description of approach used.
^c Amount of forest multiplied by habitat weight.

isons, where *m* was the number of unplanned tests. All tests were performed with a significance level of 0.05.

RESULTS

A Chi-square analysis indicated that there was a significant difference in forest age-class composition among subregions ($\chi^2 = 201.30$, *df* = 8, *P* < 0.001; Table 2). Klamath had the highest proportion of stands in younger age classes (83.7% <40 yr old) followed by Korbel (64.3% <40 yr old) and Mad River (28.7% <40 yr old).

A total of 103, 228 and 115 adult and subadult Northern Spotted Owls were banded at 55, 80 and 47 territories in the Klamath, Korbel and Mad River study areas, respectively, from 1990–97 (Fig. 1). Estimates of capture and survival probabilities were generally high and were similar among all three study areas (Table 4). The J-S model fit the data well for Klamath ($\chi^2 = 19.51$, *df* = 18, *P* = 0.361), but not for Korbel ($\chi^2 = 89.37$, *df* = 24, *P* < 0.001) and Mad River ($\chi^2 = 54.91$, *df* = 18, *P* < 0.001). We used variance inflation factors for Korbel ($\hat{c} = 3.72$) and Mad River ($\hat{c} = 3.05$) to adjust the sampling variance of the abundance estimates.

Abundance estimates appeared to increase over the first two years of the study (Fig. 2). The overall test of homogeneity for abundance estimates over the seven years yielded significant differences for Klamath ($\chi^2 = 22.80$, *df* = 6, *P* < 0.001), Korbel ($\chi^2 = 27.49$, *df* = 6, *P* < 0.001) and Mad River ($\chi^2 = 14.14$, *df* = 6, *P* = 0.028). The 1991 abundance estimates for Klamath (48.91 ± 3.65 [\pm SE]) and Korbel (117.24 ± 6.62) were significantly lower than their mean estimates for the other years,

Table 4. Jolly-Seber estimates of capture probabilities (*P*), apparent survival probabilities (ϕ) and percent coefficient of variation (CV) for mean abundance estimates of Northern Spotted Owls for three subregions of the Simpson Timber Company study area in northern California, 1991–97.

SUBREGION	<i>P</i>	SE (<i>P</i>)	ϕ	SE (ϕ)	CV (%)
Klamath	0.78	0.03	0.87	0.02	6.7
Korbel	0.84	0.01	0.88	0.01	3.1
Mad River	0.82	0.02	0.85	0.02	5.6

1992–97 (Klamath: $\bar{x} = 63.09 \pm 1.23$; $\chi^2 = 13.56$, *df* = 1, *P* < 0.001; and Korbel: $\bar{x} = 140.81 \pm 2.69$; $\chi^2 = 10.88$, *df* = 1, *P* = 0.001). The Mad River abundance estimate for 1994 (78.50 ± 4.67) was significantly different from the mean estimate for the other years ($\bar{x} = 62.82 \pm 2.00$; $\chi^2 = 9.52$, *df* = 1, *P* = 0.002). Bonferroni adjustments of the alpha level prevented identifying additional significant differences.

Empirical and J-S estimates of abundance showed similar general trends for all subregions, but there were some differences in individual estimates among some years. The confidence intervals for J-S estimates did not overlap empirical estimates of the abundance during 1992–94, 1993–96 and 1995 for Klamath, Korbel and Mad River, respectively (Fig. 2). The mean empirical and J-S estimates of abundance (Table 5) differed for Korbel ($\chi^2 = 6.805$, *df* = 1, *P* = 0.009), but were not significantly different for Klamath ($\chi^2 = 0.623$, *df* = 1, *P* = 0.430) or Mad River ($\chi^2 = 0.792$, *df* = 1, *P* = 0.373).

Mean J-S crude densities were highest for Korbel followed by Mad River and Klamath (Table 5) with an overall mean of 0.209 owls/km² (95% C.I. = 0.190–0.228). Ecological densities followed the same trend as crude densities (Fig. 2) but calculated values were higher (Table 5). Comparisons of mean crude and ecological densities indicated that the three subregions were significantly different for both variables ($\chi^2 = 2038.098$, *df* = 2, *P* < 0.001 and $\chi^2 = 1249.670$, *df* = 2, *P* < 0.001 for the crude and ecological comparisons, respectively). *Post hoc* comparisons showed crude and ecological density estimates for all subregions to be different from each other (Table 5, ecological densities: Korbel vs. Klamath; $\chi^2 = 4871.43$, *df* = 1, *P* < 0.001; Korbel vs. Mad River; $\chi^2 = 38.35$, *df* = 1, *P* < 0.001; Klamath vs. Mad River; $\chi^2 = 1679.44$, *df* = 1, *P* <

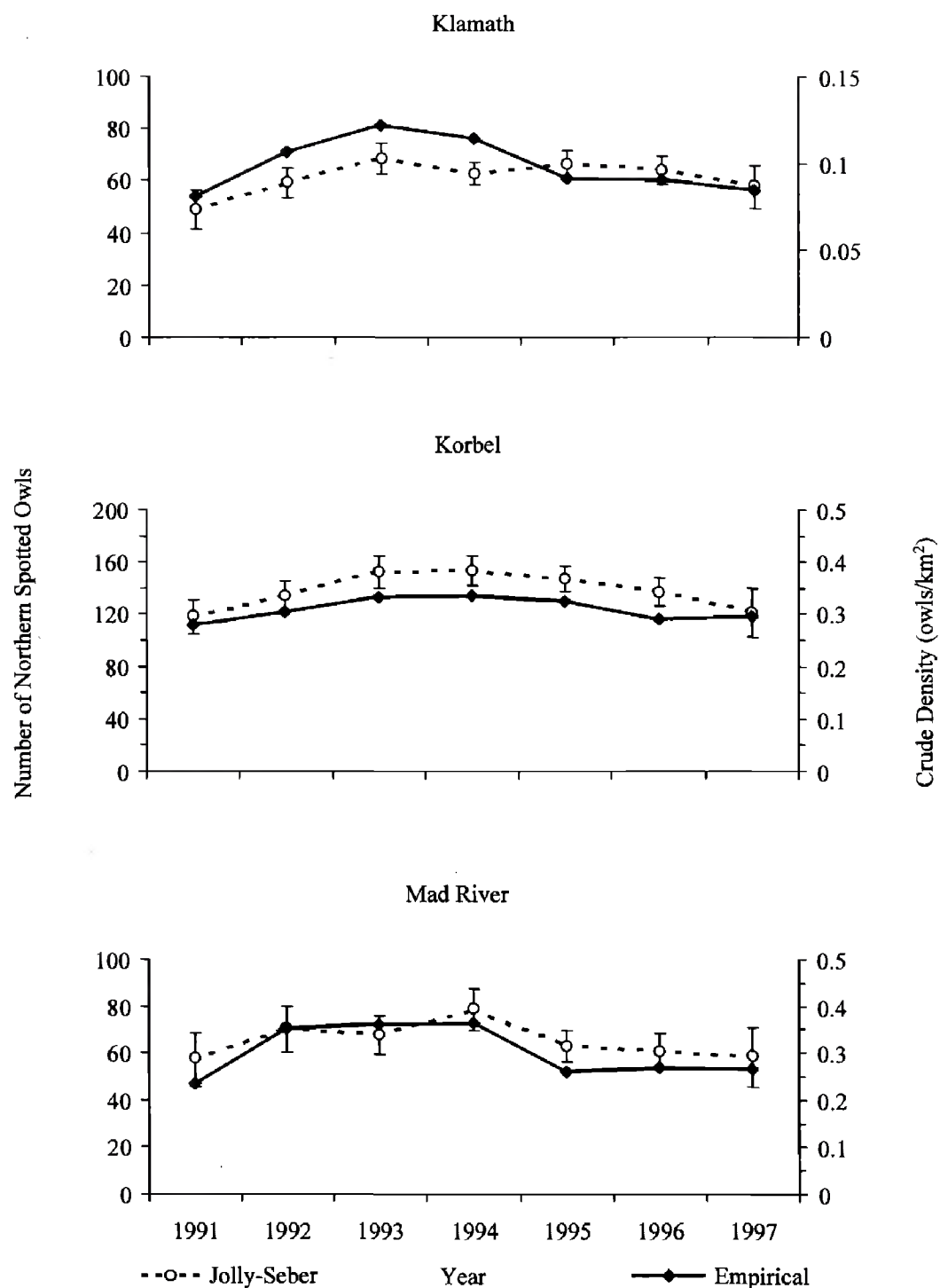


Figure 2. Number and crude density of Northern Spotted Owls on Simpson Timber Company study area subregions, northwest California. Spotted Owls were counted using mark-recapture (Jolly-Seber) and empirical methods. Bars represent 95% confidence intervals for Jolly-Seber estimates.

0.001; crude densities: Korbel vs. Klamath; $\chi^2 = 3084.67$, $df = 1$, $P < 0.001$; Korbel vs. Mad River; $\chi^2 = 1176$, $df = 1$, $P < 0.001$; Klamath vs. Mad River; $\chi^2 = 309.18$, $df = 1$, $P < 0.001$).

DISCUSSION

Others have reported that Northern Spotted Owl roost and nest sites (territory centers) tend to be located in the lower portions of drainages (Blakesley et al. 1992, Folliard 1993, Hershey et al. 1998, Lahaye and Gutiérrez 1999). In our study, many owl territories were associated with major river systems and large blocks of land without any owl territories were typically associated with major ridge-

lines or extensive areas of nonhabitat. In the Klamath and Korbel subregions, nonhabitat usually consisted of large forested areas which were too young (generally <40 yr) to support roosting or nesting, while in Mad River, extensive areas of coastal oak woodlands (Holland 1988) were considered nonhabitat.

Our smallest subregion (Mad River at 208 km²) far exceeded the minimum area of 90–130 km² estimated by Franklin et al. (1990) as necessary to provide an unbiased estimate of Northern Spotted Owl densities. However, the convoluted nature of the boundaries for this subregion may have created an edge effect that positively biased density es-

Table 5. Mean empirical and Jolly-Seber (J-S) estimates of Northern Spotted Owl abundance along with estimated crude and ecological densities for three study area subregions of the Simpson Timber Company study area in northern California, 1991–97.

SUBREGION	ABUNDANCE ESTIMATES				DENSITY ESTIMATES (OWLS/km ²)			
	EMPIRICAL		J-S		CRUDE ^a		ECOLOGICAL ^b	
	\bar{x}	\pm SE	\bar{x}	\pm SE	\bar{x}	\pm SE	\bar{x}	\pm SE
Klamath	65.6A ^c	3.95	61.1A	4.12	0.092A ^d	0	0.373A	0.015
Korbel	123.3A	3.36	137.4B	4.26	0.351B	0.014	1.049B	0.041
Mad River	60.1A	4.17	65.1A	3.63	0.313C	0.014	0.581C	0.026

^aJ-S estimates used as the dividend to calculate number of owls/total area (Odum 1971).
^bJ-S estimates used as the dividend to calculate number of owls/area of habitat (Odum 1971).
^cMeans within rows and within abundance estimates followed by the same letter do not differ ($P > 0.05$).
^dMeans within columns and within density estimates followed by the same letter do not differ ($P > 0.05$).

timates. The other subregions (Klamath at 666 km² and Korbel at 392 km²) were large enough that edge effects should not have been a factor.

This study was patterned after the Northern Spotted Owl density study by Franklin et al. (1990) in the Willow Creek study area (WCSA) immediately to the east of the Mad River subregion. They concluded that, because of the high capture and survival probabilities and the corroborative evidence provided by the empirical estimates, the J-S model provided both an accurate and precise estimate of Northern Spotted Owl density. We also found close agreement between the J-S and empirical estimates, indicating that our estimates were also accurate. The empirical estimate did significantly underestimate density relative to J-S for the Korbel subregion, but the magnitude of the difference was only 10.3%. The mean capture probability in our study area ($\bar{x} = 0.81 \pm 0.02$) was lower than that observed in the WCSA (J-S model D, $\bar{x} = 0.91 \pm 0.30$; Franklin et al. 1990), but comparisons using program CONTRAST showed no statistical differences between the two study areas ($\chi^2 = 0.103$, $df = 1$, $P = 0.748$). Comparison of mean survival probabilities between the WCSA ($\bar{x} = 0.89 \pm 0.02$; Franklin et al. 1990) and our study area ($\bar{x} = 0.87 \pm 0.01$) also showed no difference ($\chi^2 = 1.197$, $df = 1$, $P = 0.274$).

The apparent increasing abundance trend over the first few years in all subregions was most likely related to increased cumulative sampling effort and not a real increase in abundance. Despite our attempt to survey the entire study area each year, some resident owls apparently were not located until the second or even third year of the study. This conclusion was based on the observation that many

of these newly discovered owls were adult breeding pairs. If the newly discovered sites had resulted from new birds that colonized sites subsequent to the start of the study, they would most likely have been nonbreeding subadult owls. Other owls were missed in areas not surveyed in the early years of the study because they were assumed to be non-habitat but were subsequently found to contain owls.

Similar to findings reported by Franklin et al. (1990), we noted a close agreement between J-S and empirical estimates. Mean absolute differences between J-S and empirical abundance estimates were only 10.3, 7.6 and 7.4% for Korbel, Mad River and Klamath, respectively. The results of both studies could be interpreted to indicate that reliable estimates of abundance (density) can be obtained through empirical estimates without the effort and cost associated with marking and recapturing birds to obtain J-S estimates. However, we believe that if a large portion of the population is unmarked, empirical estimates would likely vary substantially due to the high potential for “double counting” individuals in some situations and discounting new birds in other circumstances. In addition, meaningful comparisons among years or study areas would be problematic because empirical estimates do not account for differences in detectability or sampling variation.

Our crude density estimates for the three subregions (Klamath—0.092 owls/km²; Korbel—0.351 owls/km²; and Mad River—0.313 owls/km²) span the reported ranges of population density for both the Northern Spotted Owl and the California Spotted Owl (*S. o. occidentalis*). Marcot and Gardetto (1980) reported the equivalent of approximately

0.325 owls/km² in the Six Rivers National Forest which is similar to our estimates for Korbelt and Mad River. However, as noted by Franklin et al. (1990), their estimate was based on empirical counts from night surveys without marking birds, and their largest study area was only 58.2 km². Both of these factors would likely positively bias their estimates making comparisons to this study problematic. The lower population density in Klamath is similar to many of the reported densities of California Spotted Owls in the Sierra and San Bernardino Mountains (Roberts 1993, Moen and Gutiérrez 1993, Lahaye and Gutiérrez 1994). Franklin et al. (1990) provided the most rigorous estimate reported for the population density of Northern Spotted Owls. They estimated a density of 0.235 owls/km² for the 292 km² WCSA, which was intermediate in study area size between the Korbelt and Mad River subregions of our study. Their estimate was similar to our combined estimate (0.209 owls/km²), but less than either Korbelt or Mad River, which were located in closest proximity to the WCSA. Tanner and Gutiérrez (1995) estimated 0.219 owls/km² for a 137.7 km² study area in Redwood National Park, which was the only previous estimate of density for Northern Spotted Owls in the coastal redwood region. This was an empirical estimate based on two years of surveys, but most owls were marked, thus the estimate was likely accurate.

Without other density studies in the coastal redwood region of Northern California, it is difficult to know the extent to which this study is representative of the region. However, we believe the pattern of density we observed was reflective of the region in general. This was based on a qualitative assessment we conducted using the 1996 California Natural Diversity Database (G. Gould, California Department of Fish and Game, unpubl. data) of reported Northern Spotted Owl locations across the entire range of the subspecies in California and on unpublished data from an adjacent large industrial land owner (S. Chinnici, Pacific Lumber Company, pers. comm.).

There was a significant difference in the amount of forested habitat in specific age classes among the three subregions. We could only speculate on how this might have influenced owl density since the study was not designed to assess this. Although some young stands (20–40 yr) in the STC study area were associated with high Northern Spotted Owl fecundity and low turnover rates, forests <40

yr old were not selected in proportion to their availability by owls for nesting (Thome et al. 1999). Thus, high proportions of stands <40 yr old might limit owl density. Klamath had significantly lower densities of owls than the other subregions along with the highest proportion of the landscape in younger stands (83.7% <40 yr old). Klamath also tended to have extensive areas of homogeneous younger age classes, although we have not quantified this difference. In comparison, Korbelt had high densities of owls, with 64.3% of forest stands <40 yr old. Based on extensive harvesting in the last 10–15 yr with relatively small clearcuts (10–24 ha), Korbelt tended to have a much more heterogeneous mixture of stand ages relative to Klamath. In the same study area, Folliard (1993) noted that landscapes supporting Northern Spotted Owls had more edge and greater stand diversity than randomly selected landscapes. Finally, like Korbelt, Mad River had high densities of owls, but only 28.7% of stands were <40 yr old. We had no data to establish a direct cause and effect relationship between habitat variables and the density of owls in the different subregions and comparing density to habitat variables was not the primary objective of this study. However, as noted by Thome et al. (1999), a combination of different age classes (older stands for nesting and younger stands for foraging) may provide the best habitat for Northern Spotted Owls in our region.

By definition, ecological densities are equal to or greater than crude densities, and one can predict that the magnitude of the difference will increase as the proportion of habitat for a given species decreases on the landscape. Ecological densities were 4.05, 2.99 and 1.86 times higher than crude densities for Klamath, Korbelt and Mad River, respectively, which supported the predicted differences based on the relative amounts of habitat in each region. In comparison, Franklin et al. (1990) reported ecological densities that were 2.81 and 2.31 times higher than crude densities depending upon the approach used for defining owl habitat.

It is difficult to make meaningful comparisons of ecological densities among studies in different areas unless the same criteria are used to calculate ecological densities. Using mature/old-growth forests to represent owl habitat, Franklin et al. (1990) reported an ecological density of 0.660 owls/km² in the WCSA. Their estimate of ecological density was greater than our estimate for the Klamath region (0.373 owls/km²), less than Korbelt (1.049

owls/km²) but quite similar to Mad River (0.581 owls/km²). In addition to being closest in proximity to the WCSA, Mad River also had the highest proportion of mature stands (36.9% >80 yr in age, although it lacked old growth habitat) compared to 35.6% mature/old growth in the WCSA.

There is some question as to the extent comparisons of Northern Spotted Owl densities, either within or between study areas, can be used for developing management prescriptions. As noted by Van Horne (1983), population density of a species can be a misleading indicator of habitat quality. Although some of the attributes of Northern Spotted Owl populations do not meet the criteria for habitat quality-density decoupling, a prediction consistent with decoupling habitat quality and density is that high owl densities on selected managed lands result from displacement of owls from adjacent harvested areas. However, we believe this was unlikely because the densities in our study area appeared to be relatively stable throughout a time period when, due to its federally-listed status (USDI 1992), significant habitat alteration of Northern Spotted Owl habitat was not permitted on adjacent private lands. In addition, there was a 90–95% reduction in annual timber harvest on adjacent public land (Six Rivers National Forest) just prior to and after the listing of the Northern Spotted Owl (USDA 1995). Finally, we have observed that the highest reproduction tends to be associated with areas of highest densities (L. Diller, unpubl. data), but it was beyond the scope of this study to quantify the relationship between reproduction and density.

Although it was unlikely that the densities of owls in our study area were influenced by displacement from adjacent areas, we could not assess habitat quality in our study area based on density of owls. First and foremost, we could not establish causal relationships between the observed differences in density and corresponding differences in habitat attributes without undertaking an experimental approach over large areas. Correlative studies to elucidate patterns between habitat attributes and density were not possible when only a few sub-regions were available for comparison. In addition, we could only estimate the density of the territorial population of owls, and true density, which would include nonterritorial floaters, was unknown. Given the difficulty of undertaking experiments with a protected species over large areas, we believe that more immediate insight can be gained concerning

habitat quality by relating demographic parameters to habitat attributes in a manner described in Thome et al. (1999). Ultimately, knowing population density is of limited immediate benefit for developing conservation strategies for Northern Spotted Owls without knowing the habitat attributes that result in demographic parameters that will sustain populations over time. However, establishing reliable estimates of population densities for Northern Spotted Owls should provide valuable baseline data for assessing long-term trends in their populations. Similar studies should be conducted in selected areas throughout the range of the Northern Spotted Owl to allow future assessment of the long-term response of this species to current management strategies now being implemented.

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LITERATURE CITED

- ANDERSON, D.R., K.P. BURNHAM AND G.C. WHITE. 1994. AIC model selection in overdispersed capture-recapture data. *Ecology* 75:1780–1793.
- BART, J. AND E.D. FORSMAN. 1992. Dependence of Northern Spotted Owls *Strix occidentalis caurina* on old-growth forests in the western USA. *Biol. Cons.* 62:95–100.
- BLAKESLEY, J.A., A.B. FRANKLIN AND R.J. GUTIÉRREZ. 1992. Spotted Owl roost and nest-site selection in northwestern California. *J. Wildl. Manage.* 56:388–392.
- BURNHAM, K.P., D.R. ANDERSON, G.C. WHITE, C. BROWNIE AND K.H. POLLOCK. 1987. Design and analysis methods for fish survival experiments based on release-recapture. *Am. Fish. Soc. Monogr.* 5.
- CAREY, A.B., J.A. REID AND S.P. HORTON. 1990. Spotted Owl home range and habitat use in southern Oregon Coast Ranges. *J. Wildl. Manage.* 54:11–17.
- , S.P. HORTON AND B.L. BISWELL. 1992. Northern Spotted Owls: influence of prey base and landscape character. *Ecol. Monogr.* 62:223–250.
- CAUGHLEY, G. AND A. SINCLAIR. 1994. Wildlife ecology and management. Blackwell Scientific Publications, Cambridge, MA U.S.A.
- ELFORD, R.C. 1974. Climate of Humboldt and Del Norte counties. Humboldt and Del Norte Counties Agric. Exten. Serv., Univ. California, Davis, CA U.S.A.

- FOLLIARD, L.B. 1993. Nest-site characteristics of Northern Spotted Owls in managed forests of northwest California. M.S. thesis, Univ. Idaho, Moscow, ID U.S.A.
- FORSMAN, E.D. 1981. Molt of the Spotted Owl. *Auk* 98: 735-742.
- . 1983. Methods and materials for locating and studying Spotted Owls. USDA For. Serv. Gen. Tech. Rep. PNW-162, Portland, OR U.S.A.
- . 1988. A survey of Spotted Owls in young forests in the northern coast range of Oregon. *Murrelet* 69: 65-68.
- , E.C. MESLOW AND M.J. STRUB. 1977. Spotted Owl abundance in young versus old-growth forests. *Oreg. Wildl. Soc. Bull.* 5:43-47.
- , ——— AND ———. 1984. Distribution and biology of the Spotted Owl in Oregon. *Wildl. Monogr.* 87: 1-64.
- , C.R. BRUCE, M.A. WALKER AND E.C. MESLOW. 1987. A current assessment of the Spotted Owl population in Oregon. *Murrelet* 68:51-54.
- , A.B. FRANKLIN, F.M. OLIVER AND J.P. WARD. 1996. A color band for Spotted Owls. *J. Field Ornithol.* 67: 507-510.
- FRANKLIN, A.B., J.P. WARD, R.J. GUTIÉRREZ AND G.I. GOULD, JR. 1990. Density of Northern Spotted Owls in northwest California. *J. Wildl. Manage.* 54:1-10.
- GUTIÉRREZ, R.J., E.D. FORSMAN, A.B. FRANKLIN AND E.C. MESLOW. 1996. History of demographic studies in the management of the Northern Spotted Owl. *Stud. Avian Biol.* 17:6-11.
- HERSHEY, K.T., E.C. MESLOW AND F.L. RAMSEY. 1998. Characteristics of forests at Spotted Owl nest sites in the Pacific Northwest. *J. Wildl. Manage.* 62:1398-1410.
- HINES, J.W. AND J.R. SAUER. 1989. Program CONTRAST—A general program for the analysis of several survival or recovery rate estimates. USDI Fish and Wildl. Serv., Tech. Rep. 24, Washington, DC U.S.A.
- HINTZE, J.L. 1997. NCSS 97: Statistical system for windows. NCSS, Kaysville, UT U.S.A.
- HOLLAND, V.L. 1988. Coastal oak woodland. Pages 78-79 in K.E. Mayer and W.F. Laudenslayer, Jr. [EDS.], A guide to wildlife habitats of California. USDA Forest Service, Sacramento, CA U.S.A.
- INTERGRAPH CORPORATION. 1994. MGE base mapper reference manual. Intergraph, Huntsville, AL U.S.A.
- JOLLY, G.M. 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. *Biometrika* 52:225-247.
- . 1982. Mark-recapture models with parameters constant in time. *Biometrics* 38:301-321.
- KREBS, C.J. 1985. Ecology: the experimental analysis of distribution and abundance. Harper and Row, New York, NY U.S.A.
- LAHAYE, W.S. AND R.J. GUTIÉRREZ. 1994. Big Bear Spotted Owl study, 1993. Calif. Dept. of Fish and Game, Nongame Bird and Mammal Section. Tech. Rep. 1994-3, Sacramento, CA U.S.A.
- AND ———. 1999. Nest sites and nesting habitat of the Northern Spotted Owl in northwestern California. *Condor* 101:324-330.
- LEBRETON, J.-D., K.P. BURNHAM, J. CLOBERT AND D.R. ANDERSON. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol. Monogr.* 62:67-118.
- MARCOT, B.G. AND J. GARDETTO. 1980. Status of the Spotted Owl in Six Rivers National Forest. *West. Birds* 11: 79-87.
- AND J.W. THOMAS. 1997. Of Spotted Owls, old growth, and new policies: a history since the Interagency Scientific Committee Report. USDA For. Serv. Gen. Tech. Rep. PNW-408, Portland, OR U.S.A.
- MAYER, K.E. 1988. Redwood. Pages 60-61 in K.E. Mayer and W.F. Laudenslayer, Jr. [EDS.], A guide to wildlife habitats of California, USDA Forest Service, Sacramento, CA U.S.A.
- MCCULLAGH, P. AND J.A. NELDER. 1989. Generalized linear models. Chapman and Hall, New York, NY U.S.A.
- MOEN, C.A., A.B. FRANKLIN AND R.J. GUTIÉRREZ. 1991. Age determination of subadult Northern Spotted Owls in northwest California. *Wildl. Soc. Bull.* 19:489-493.
- AND R.J. GUTIÉRREZ. 1993. Population ecology of the California Spotted Owl in the central Sierra Nevada: annual results, 1992. Calif. Dept. of Fish and Game, Nongame Bird and Mammal Section. Tech. Rep. 1993-14, Sacramento, CA U.S.A.
- NETER, J. AND W. WASSERMAN. 1974. Applied linear statistical models. Richard D. Irwin, Homewood, IL U.S.A.
- ODUM, E.P. 1971. Fundamentals of ecology. Saunders College Publ., Philadelphia, PA U.S.A.
- POLLOCK, K.H., J.E. HINES AND J.D. NICHOLS. 1985. Goodness-of-fit tests for open capture-recapture models. *Biometrics* 41:399-410.
- , J.D. NICHOLS, C. BROWNIE AND J.E. HINES. 1990. Statistical inference for capture-recapture experiments. *Wildl. Monogr.* 107:1-97.
- ROBERTS, C.K. 1993. California Spotted Owl (*Strix occidentalis caurina*) inventory and demographic study, Sequoia and Kings Canyon National Parks: final 1988-89. Calif. Dept. of Fish and Game, Nongame Bird and Mammal Section. Tech. Rep. 1993-4, Sacramento, CA U.S.A.
- SAUER, R.J. AND B.K. WILLIAMS. 1989. Generalized procedures for testing hypotheses about survival or recovery rates. *J. Wildl. Manage.* 53:137-142.
- SEBER, G.A.F. 1965. A note on the multiple recapture census. *Biometrika* 52:249-259.
- . 1982. The estimation of animal abundance and related parameters. Charles Griffin and Co., London, U.K.
- SIMPSON TIMBER COMPANY. 1992. Habitat conservation plan for the Northern Spotted Owl on the California timberlands of Simpson Timber Company. Simpson Timber Company, Korbel, CA U.S.A.
- SOLIS, D.M., JR. AND R.J. GUTIÉRREZ. 1990. Summer hab-

- itat ecology of Northern Spotted Owls in northwestern California. *Condor* 92:739–748.
- TANNER, R.G. AND R.J. GUTIÉRREZ. 1995. A partial inventory of Northern Spotted Owls (*Strix occidentalis caurina*) in Redwood National Park, 1994. Unpubl. Rep., Arcata, CA U.S.A.
- THOMAS, J.W., E.D. FORSMAN, J.B. LINT, E.C. MESLOW, B.R. NOON AND J. VERNER. 1990. A conservation strategy for the Northern Spotted Owl. U.S. Gov. Printing Off., Washington, DC U.S.A.
- THOME, D.M., C.J. ZABEL AND L.V. DILLER. 1999. Forest stand characteristics and reproduction of Spotted Owls in managed north-coastal California forests. *J. Wildl. Manage.* 63:44–59.
- USDA. 1995. Land and resource management plan for the Six Rivers National Forest: final environmental impact statement. Eureka, CA U.S.A.
- USDI. 1992. Draft recovery plan for the Northern Spotted Owl. USDI Fish and Wildl. Serv., Portland, OR U.S.A.
- VAN HORNE, B. 1983. Density as a misleading indicator of habitat quality. *J. Wildl. Manage.* 47:893–901.
- ZINKE, P.J. 1988. The redwood forest and associated north coast forests. Pages 679–698 in M.G. Barbour and J. Major [EDS.], *Terrestrial vegetation of California*. Univ. of Calif. Davis, Davis, CA U.S.A.

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BREEDING BIOLOGY OF THE SHORT-EARED OWL (*ASIO FLAMMEUS*) IN AGRICULTURAL HABITATS OF SOUTHWESTERN FRANCE

BEATRIZ E. ARROYO AND VINCENT BRETAGNOLLE
CNRS-CEBC, 79360 Beauvoir sur Niort, France

ABSTRACT.—Long-term studies of the Short-eared Owl (*Asio flammeus*) have been conducted mainly in its central breeding range. We studied its breeding biology in an agricultural habitat in southwestern France, at the southern edge of its breeding range in Europe. The abundance of the main prey species, the common vole (*Microtus arvalis*), varied cyclically. Between 1994–98, breeding was only confirmed in 1996, a peak vole year, when 13–19 pairs bred in cereal crop and rye-grass fields. In that year, breeding success was high ($\bar{x} = 5.7 \pm 0.9$ [\pm SD] fledglings per pair), although some young had to be temporarily removed from fields to avoid mortality due to harvesting or mowing activities. The distribution of breeding pairs was clumped. Land use around Short-eared Owl nests included significantly more cereal and semipermanent crops (the two cover types with the highest vole densities in 1996) than expected from random. The spatial distribution of Short-eared Owls was, however, not entirely explained by vole abundance, as there was an apparent nonrandom spatial association with breeding harriers (*Circus* spp).

KEY WORDS: *Short-eared Owl*; *Asio flammeus*; *agricultural habitat*; *breeding success*; *conservation*.

Biología reproductiva de la lechuza campestre (*Asio flammeus*) en una zona agrícola del sudoeste de Francia

RESUMEN.—La mayoría de los estudios a largo plazo sobre la Lechuza Campestre (*Asio flammeus*) se han realizado en el centro de su área de distribución. En este artículo, describimos la biología reproductiva de esta especie en un hábitat agrícola en el sudoeste de Francia, al límite sur del área de distribución de la especie en Europa. La abundancia de la presa principal, el topillo campestre (*Microtus arvalis*) fluctúa cíclicamente en la zona de estudio. En el periodo 1994–98, la reproducción sólo se confirmó en 1996, un año de sobre-abundancia de topillos, en el que entre 13 y 19 parejas criaron en campos de cereal y de centeno. El éxito reproductor en ese año fue elevado ($\bar{x} = 5.7 \pm 0.9$ [\pm DE] pollos por pareja) aunque algunos pollos tuvieron que retirarse temporalmente para evitar su muerte debido a la siega. La distribución espacial de los nidos no fue aleatoria, sino significativamente agregada. En un radio de 500 m alrededor de los nidos de Lechuza Campestre había significativamente más cereal y cultivos semipermanentes (los dos tipos de cubierta vegetal con mayores densidades de topillo en 1996) que lo esperado según la disponibilidad de ambos. No obstante, la abundancia de topillos no explicaba enteramente la distribución espacial de la Lechuza Campestre, ya que se observó una asociación aparentemente no aleatoria entre los nidos de esa especie y los nidos de aguilucho (*Circus* spp).

[Traducción de Autor]

Short-eared Owls (*Asio flammeus*) usually breed in high arctic to mid-latitudes both in the Old and New Worlds (Cramp 1985, Holt and Leasure 1993). The strong relationship of Short-eared Owls with vole-like mammals in the breeding and wintering range is well-known (Mikkola 1983, Korpimäki 1984, Wiebe 1991, Rau et al. 1992, Holt 1993). Most studies of breeding Short-eared Owls have been conducted within the main breeding range of the species and have concentrated on the relationship between vole abundance and owl breeding numbers, success or territory size (Lockie

1955, Clark 1975, Mikkola 1983, Korpimäki 1984, Village 1987, Korpimäki and Norrdahl 1991, Holt 1992). Nonetheless, Short-eared Owls are nomadic (Mikkola 1983, Holt and Leasure 1993) and may leave their traditional areas to breed elsewhere when prey is scarce and/or when rodent density is high elsewhere (Beske and Champion 1971, Hölzinger et al. 1973, Mikkola 1983). Fluctuations in Short-eared Owl numbers are also marked at the edge of their breeding range, where breeding occurs only irregularly, and data from such areas are very scarce (Beske and Champion 1971, Hölzinger

et al. 1973, Jubete et al. 1996). The comparison of breeding parameters between areas at the center and edge of the breeding range may help to discriminate two hypotheses regarding Short-eared Owl invasions. First, owls invade suboptimal areas as a response to the lack of food in their main area, because it is better to breed in suboptimal areas than not to breed at all (Hölzinger et al. 1973) and second, owls can track changes in vole populations without time lag, thus occupying edge areas because they become optimal at different times (Korpimäki and Norrdahl 1991).

The usual breeding habitats for the Short-eared Owl are open grasslands, moorland heaths, marshes, grassy moorlands, pine plantations and tundra areas (Mikkola 1983, Cramp 1985, Holt and Leasure 1993). However, outside the main breeding range and during vole outbreaks, they also nest in agricultural habitats (Holt and Leasure 1993, Jubete et al. 1996, Yeatman-Berthelot and Jarry 1994, Michelat 1997). The consequences of this habitat choice, in terms of breeding success, are basically unknown. Only Jubete et al. (1996) specified that breeding success in an agricultural habitat was greatly reduced due to harvesting activities.

In this paper, we describe the breeding biology of the Short-eared Owl in an agricultural habitat in southwestern France, at the southern edge of its breeding range. We report on breeding success and behavior, nest dispersion, habitat selection and feeding rates, and compare our results with other published data, discussing the implications for the species of breeding in an edge area and in an agricultural habitat.

STUDY AREA AND METHODS

The study area was located in the Département des Deux Sèvres, westcentral France (46°11'N, 0°28'W) and covered about 340 km² of agricultural habitat. Land use was represented by a mixture of winter cereal crops (ca. 35% of the surface), oil rape-seed crops (ca. 10%), spring-sown crops (sunflower and corn, ca. 25%), pasture (ca. 5%), semipermanent crops dedicated to livestock rearing, such as alfalfa, rye-grass or hay fields (ca. 10%), other crops such as peas, vineyards or flax (ca. 5%) and nonagricultural cover (villages and forest, ca. 10%). From 1994–98, five to 15 people searched the study area daily from April–August for breeding pairs of harrier species (*Circus spp.*), Little Bustards (*Tetrax tetrax*) and Stone Curlews (*Burhinus oedipnemus*). They recorded all observations of Short-eared Owl individuals or pairs.

We defined certain breeding pairs as those for which reproductive behavior was observed: either a nest was found ($N = 6$), a fledged family was observed ($N = 3$), or prey deliveries between males and females were ob-

served ($N = 4$). Observations of pairs in a given area more than once, but where none of these behaviors could be detected, were considered to be possible breeding pairs. All reproductive data (habitat selection, reproductive success and feeding rates) were from 1996, the only year when breeding was confirmed. Nests were located through triangulation. Two observers were placed at different points and they simultaneously watched males or females coming into nests with prey. Nests were subsequently visited by a third person to record clutch or brood size. Nests were visited one to eight times during the breeding season and crop height was measured at the nest during the first visit. We measured egg width and length with vernier calipers to 0.1 mm. Laying date was estimated by backdating from hatching date assuming a 26 d incubation period (Gröndlund and Mikkola 1969). Hatching dates were known in three cases or estimated through nestling age in the others. Prey deliveries were also used to locate and trap nestlings in the field after their dispersal from nests. Nestlings were measured, banded and released at the same spot, except when they were at risk from harvesting activities. If crops were about to be harvested or mowed, we temporarily removed the nestlings, took them to a lab and then released them at the original spot after harvesting. Removals were short (4 to 7 d) and, in most cases, not all nestlings from a brood were removed because we could not find some of them. Parents did not desert the area and kept feeding nestlings after their release from the lab.

Feeding activity rhythm was assessed by means of focal sampling observations on six different pairs for a total of 20 evenings (2100–2300 H) from 29 May–27 July, totaling ca. 20 hr of observations. Two of these pairs were also observed at night (2200–0200 H) with a light amplifier (one night each). At another nest, observations were carried out twice before dawn (0400 H onwards).

The spatial distribution of all pairs found in 1996 was assessed using the nearest neighbor method (Clark and Evans 1954, Krebs 1989). The expected distance to the nearest neighbor in a population with a random spatial pattern is defined by $r_E = 1/2\sqrt{\rho}$ (where ρ = density). The ratio R (r_A/r_E , where r_A is the observed distance to the nearest neighbor) provides an index of aggregation of individuals with R values lower than 1 indicating increasing levels of clumping. The significance of the deviation from randomness was tested from the standard normal deviate $z = (r_A - r_E)/s_r$ where $s_r = 0.26136/\sqrt{np}$ is the standard error of the expected distance to the nearest neighbor (Krebs 1989).

Land use of the study area was determined in the field and data were then entered to Geographical Information System software (ArcView 3.0a). To evaluate habitat preference, we used a 500 m circle around the location of each pair and determined the land use in each of the circles (total area of each of the described cover types). These data were compared with the area available in the whole study area using chi-square tests. To evaluate which habitats were preferred or avoided, we assessed how each expected proportion of cover type deviated from the null hypothesis (Neu et al. 1974) by inspecting the standard residuals of each theoretical proportion of occurrence in the chi-square table. As standard residuals follow a normal distribution, standard residuals higher than 1.95 in-

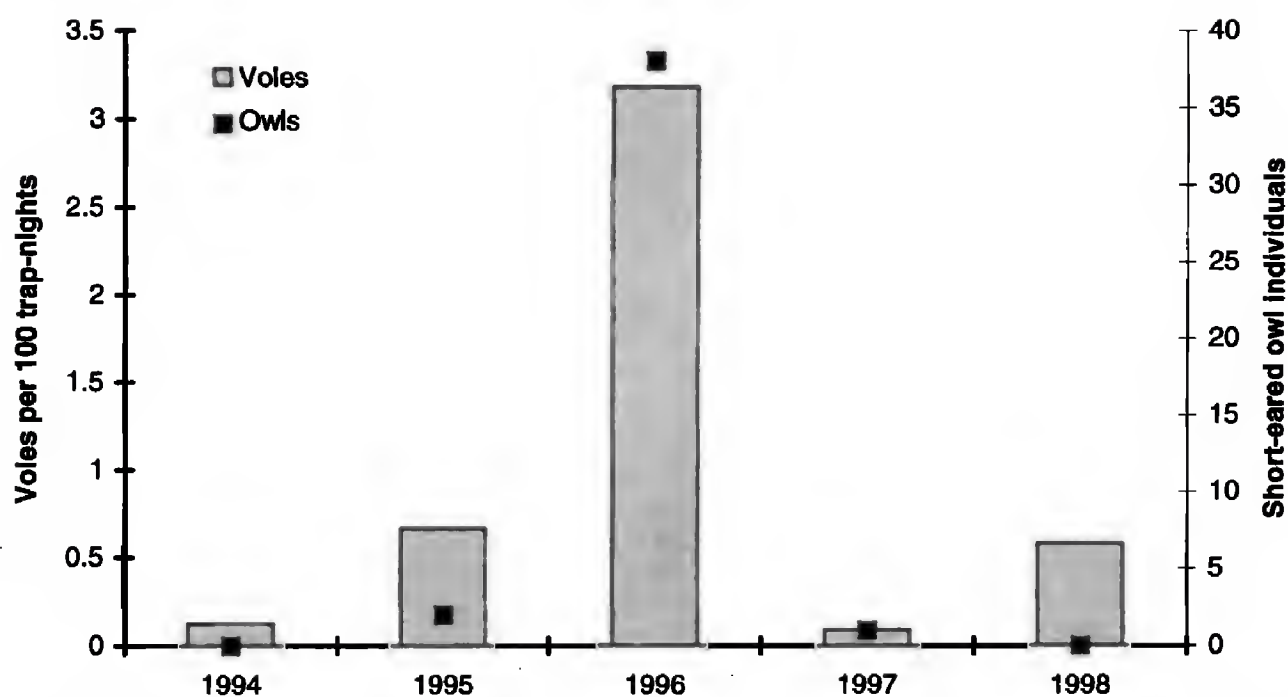


Figure 1. Estimated number of Short-eared Owls recorded during the breeding period (April–August) from 1994–98, and vole abundance in the same period.

dicated that observed proportions deviated significantly from expected values at the 0.05 level.

Vole abundance was estimated in April and July with trap lines, using snap traps. This procedure was considered appropriate for assessing the amplitude of fluctuations of the main prey species, the common vole (*Microtus arvalis*) (Spitz et al. 1974, Spitz 1977, Delattre et al. 1992). Each trap line was 100 m long and had 51 unbaited traps spaced every 2 m (Butet and Leroux 1993). One trap line was placed in each habitat type. The percent of traps in each cover type was similar each year. Traps were checked and removed 24 hr after their set-up. There were approximately 8000 trap-nights each year from 1995–98. In 1994, there were only 1224 trap-nights. Results of trapping are expressed as the number of vole captures per 100 trap-nights.

RESULTS

Variation in Short-eared Owl Numbers. No Short-eared Owls were observed in the study area during the breeding season in 1994 and 1998. An unpaired individual was observed in 1997. A breeding attempt was suspected in 1995 after a pair was observed defending a territory against raptor intruders. Reproduction of Short-eared Owls was verified only in 1996 when 13–19 pairs bred within the study area. That year was a peak vole year and the vole capture rate was five times higher than in intermediate years, and 30 times higher than in low vole years (Fig. 1). Overall, the number of breeding or nonbreeding Short-eared Owls recorded in the study area during breeding seasons from 1994–98 followed the abundance of common voles closely (Fig. 1), but the relationship was not signif-

icant (Spearman rank correlation, $r_s = 0.667$, $N = 5$, $P > 0.1$).

Breeding Habitat and Reproductive Parameters. Six nests of the 13 breeding pairs detected in 1996 were found. Fledging success and laying dates were also available for three other pairs. Only the locations of the remaining four pairs were known. Of the six nests found, one of them was in a rye-grass field and five in winter cereal crops.

Laying took place between 4 April and 6 May. Median laying date was 20 April ($N = 9$). Fledged young were still fed by their parents up to 61 ± 11 (\pm SD) d after hatching ($N = 5$ broods) but all owls left the area by August. No second broods were observed.

Mean clutch size was 8.0 ± 1.1 for nests visited at egg stage ($N = 4$). Mean egg length was 39.0 ± 0.8 mm, and mean egg width 31.4 ± 0.6 mm ($N = 8$ eggs). Brood size in these four nests was 7.5 ± 1.3 . Brood size at first visit for the other two nests was six and seven. Young apparently hatched at 1- or 2-d intervals based on nestling measurements. They dispersed from nests at 13 ± 2 d of age (range = 9–16 d, $N = 16$ young) so we found young ≤ 100 m from nests when eggs were still being incubated. Because nestlings dispersed in all directions, successive prey deliveries to very different sites allowed us to quantify the minimum number of living young. One clutch was collected because of mowing activities and incubated artificially. The five young that were raised were

released when they reached normal fledging age. Additionally, a minimum of 46 young fledged in the study area, 16 of which were temporarily removed before harvesting. Thus, mean productivity ranged between 5.7 ± 0.9 – 3.9 ± 2.6 ($N = 9$) young per pair, the latter value obtained by assuming that all nestlings temporarily removed during harvesting or eggs incubated artificially would have died without intervention.

Feeding Rates. Nestlings were fed by males when females were still incubating or brooding, and by both parents thereafter, although we could not gather data on the relative contribution of each sex. In general, feeding took place just after sunset (93% of 77 observed prey deliveries). Four other prey deliveries were observed in the hour immediately before sunset in only three of the 20 focal nest observations. Mean feeding rates at sunset during the nestling period were 5.76 ± 1.9 prey deliveries per hour. We never observed any feeding or hunting activity in daylight, and therefore could not report on hunting distances or territory sizes. However, the short interval between prey deliveries (ca. 10 min.) suggested that most of the hunting was done very close to nests. After 2300 H, prey deliveries were very rare and only one prey delivery was seen during observations at night. Similarly, we did not see any food delivery early in the morning indicating that young were fed exclusively in the evening when each young received on average 1.14 ± 0.63 voles per hour. Assuming that the total hunting time of adults was limited to 2 hr each day from sunset to 2300 H, each nestling received a total of 2–3 voles per day.

Nest Spacing and Habitat Selection. Short-eared Owl pairs in 1996 were not randomly distributed, but significantly clumped ($R = 0.44$, $z = -3.85$, $P = 0.001$; Fig. 2). All breeding pairs were concentrated in an area of about 125 km², where density reached 0.10–0.15 pairs/km², and where vole abundance in April was high relative to the whole study area (Fig. 2). Clumped nest distribution was marginally significant if the test was conducted only with data from the highest density area ($R = 0.73$, $z = -1.88$, $P = 0.06$). Mean distance to the nearest neighbor was 1120 ± 883 m ($N = 13$, range = 350–2700 m), or 1692 ± 1666 m if we included the six probable breeding pairs.

Overall, the distribution of breeding sites was apparently related to food abundance. The western side of the study area, where Short-eared Owls were absent, showed the lowest values of vole cap-

ture rate in April (Fig. 2). Furthermore, the average proportion of different crop types within 500 m of breeding sites was significantly different from that available in the study area ($\chi^2_6 = 144$, $P < 0.001$). Cereal and semipermanent crops, where voles were highly abundant, were significantly more frequent around nests than expected based on their availability (Table 1). In contrast, pasture and spring-sown crops, where voles were very scarce, were significantly avoided together with inhabited areas (Table 1). Land use varied significantly among Short-eared Owl nest areas ($\chi^2_{72} = 5326$, $P < 0.0001$), but cereal and semipermanent crops were more represented than expected by random in 10 and 11, respectively, of the 13 nest areas. This suggested that nest location was mainly influenced by food abundance and availability.

There was an apparently nonrandom link between Short-eared Owl and harrier nest locations. At least one harrier nest was located within 500 m of owl nests in 10 of 13 cases. For these 10 pairs, mean number of nearby breeding harriers was 2.6 ± 1.3 (range = 1–4) and mean minimum distance to a harrier nest was 230 ± 156 m. Harriers breeding near Short-eared Owls were mainly Montagu's Harriers (*Circus pygargus*), which were particularly abundant in the study area in 1996, but Marsh Harriers (*C. aeruginosus*) and Hen Harriers (*C. cyaneus*) bred nearby on one and two occasions, respectively. Interspecific agonistic contacts between Short-eared Owls and harriers were frequently observed at seven of the 10 nests. In contrast, intraspecific agonistic behavior was rarely observed, even in the areas where several owl nests were located within 500 m of each other, although the owls seemed to avoid each other by hunting in opposite directions from their nests.

DISCUSSION

Owl Outbreaks, Vole Abundance and Breeding Success. Hölzinger et al. (1973) suggested that Short-eared Owls leave their regular breeding quarters in northern Europe when prey supply is scarce, moving to southwestern areas with high vole populations and returning northwards in subsequent breeding seasons. Alternatively, owls may track high density vole areas without a time lag and establish territories in areas where expected breeding success is highest (Korpimäki and Norrdahl 1991).

Short-eared Owls winter regularly in western France (Yeatman-Berthelot and Jarry 1991), in-

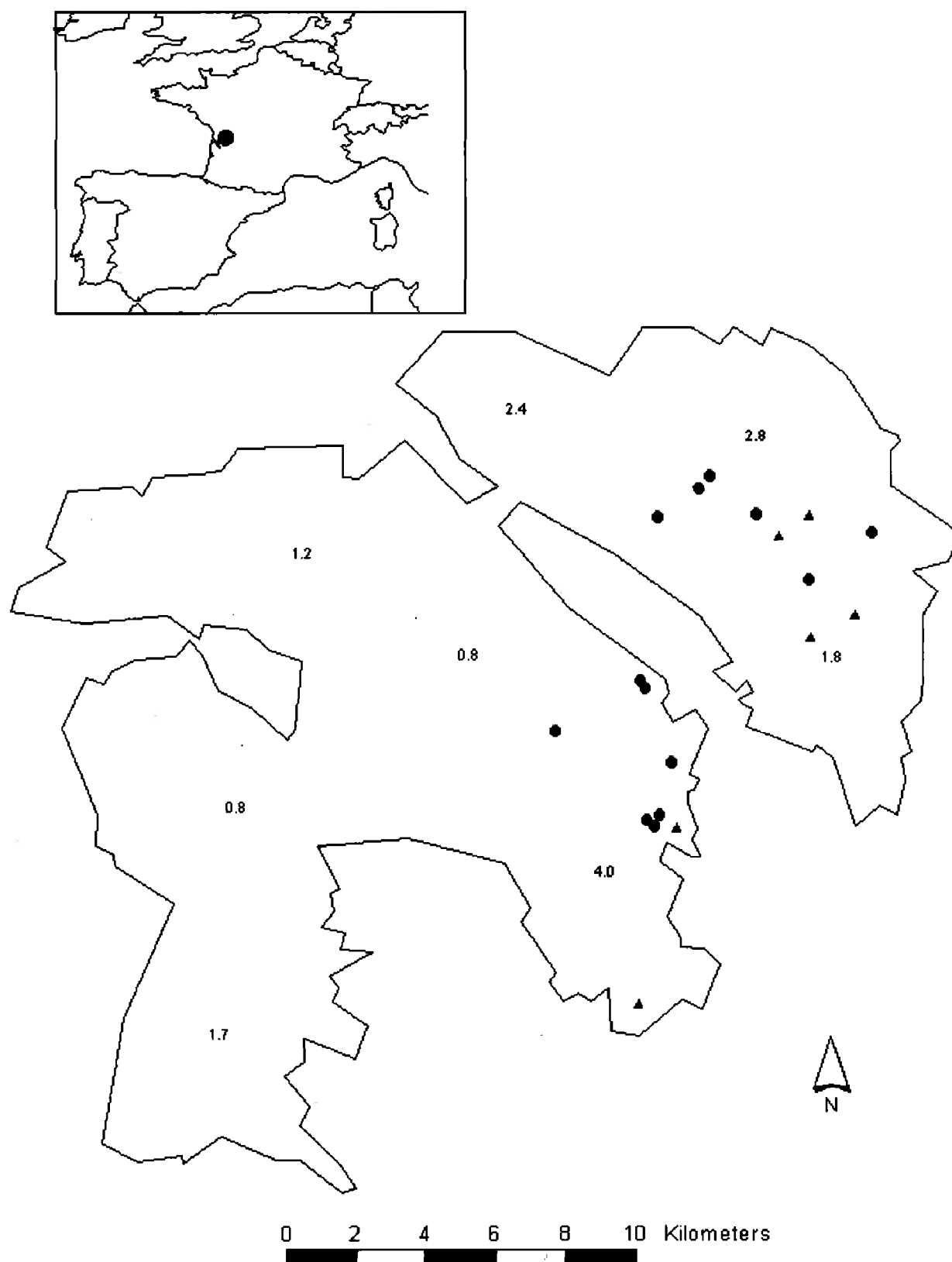


Figure 2. Distribution of breeding pairs of Short-eared Owls in 1996. Circles show confirmed breeding pairs and triangles show probable breeding pairs. Numbers refer to the average vole abundance (captures/100 traps) in April in different sectors of the study area.

cluding our study area, but they remained to breed only in 1996, a peak vole year. In France, another outbreak of breeding Short-eared Owls was observed in 1993 which was also a vole peak year (Michelat 1997, pers. obs.). In that year, 48–134 pairs nested in France, sometimes inland, which was atypical (Michelat 1997). Similarly, in Spain, where the species rarely nests (Asensio et al. 1992), ≤ 400 pairs were estimated to breed in 1993–94 when a vole irruption occurred (Jubete et al.

1996). In Spain, breeding areas also corresponded to regular wintering areas (Asensio et al. 1992, Jubete et al. 1996). These results suggested that Short-eared Owls may remain near their wintering areas if conditions for nesting are good, rather than dispersing from northern breeding areas when prey is low as proposed by Hölzinger et al. (1973).

Nesting success in edge areas is generally low. In Germany, breeding success was 27% with an average of 1.94 fledglings per pair ($N = 17$, Hölzinger

Table 1. Mean (\pm SD) height (cm), and vole abundance (captures/100 trap-nights) of different cover types measured in April 1996. Sample size (number of fields sampled) is shown in brackets. Cover type availability (% of total surface) in the study area and mean (\pm SD) proportion in 13 Short-eared Owl nesting locations is also expressed. The standard residuals of each theoretical proportion of occurrence (from the chi-square table) indicate how observed data deviate from the null hypothesis (proportion observed = expected).

COVER TYPE	HEIGHT	VOLE ABUNDANCE	AVAIL- ABILITY	PRESENCE IN SHORT-EARED OWL TERRITORIES	STANDARD RESIDUALS
Winter cereal	46.7 \pm 10.9 (15)	9.1 \pm 12.3 (17)	35	43.5 \pm 13.6	4.12
Oil rape-seed	127.3 \pm 13.5 (8)	6.8 \pm 4.8 (8)	10	10.8 \pm 8.7	0.83
Spring-sown crops	3.9 \pm 10.8 (9)	1.6 \pm 2.4 (9)	26	20.4 \pm 15.7	-2.87
Pasture	29.2 \pm 13.0 (11)	1.9 \pm 3.0 (10)	5	0.6 \pm 1.5	-5.35
Semipermanent crops	33.2 \pm 16.3 (40)	12.9 \pm 5.5 (42)	10	17.1 \pm 9.7	6.22
Other crops	—	—	5	5.4 \pm 8.3	0.51
Nonagricultural cover	—	—	10	2.1 \pm 3.8	-6.89

et al. 1973). In Wales, clutch size was low at 5.8 ± 0.8 eggs ($N = 5$); average fledging success per successful pair was 3.0 young and few pairs produced fledglings due to heavy losses between laying and fledging (Lawton and Bowman 1986). In Spain, productivity was also low averaging only 1.87 fledged young per pair (range 1–10, $N = 39$; Jubete et al. 1996). Mean fledged brood size in France in 1993 was 2.7 ± 1.2 ($N = 30$), but that figure did not include nests that failed before fledging (Michelat 1997). In contrast, breeding success in areas located within the main breeding range is much higher. In western Finland, mean productivity was 3.1 ± 2.3 young (range = 1.3–4.1, $N = 78$ pairs over 5 yr, Korpimäki 1984). In the northeastern U.S., mean fledging success was 3.2 ± 2.2 ($N = 9$, Holt 1992). This indicates that owls do not track the best areas. However, in our study area, breeding success in 1996 was much higher than that reported for other southern edge areas and similar to that found in the main breeding areas. Similarly, breeding success was also high in another southern edge area, the Buena Vista Marsh (Beske and Champion 1971), with an average of five fledglings per pair and up to 10 fledged from a single nest (70 young from 14 successful pairs). The latter study took place in a year when the vole population was particularly high compared with other vole peaks (Beske and Champion 1971). Therefore, we suggest that breeding at edge areas may be sub-

optimal given the low average breeding success in these areas unless food conditions are exceptionally good, and are not preferred unless prey abundance in wintering areas is so exceptional that expected breeding success is high. It should be noted that the latter explanation does not rely on knowing prey levels in usual breeding areas. Data on between-year movements of individual birds would be needed to validate this hypothesis.

Breeding in Agricultural Habitats and Conservation. The use of agricultural habitats by breeding Short-eared Owls is relatively uncommon except during vole outbreaks (Mikkola 1983, Holt and Leasure 1993). It seems more common outside than inside the main breeding range (Holt and Leasure 1993, Jubete et al. 1996, Yeatman-Berthelot and Jarry 1994, Michelat 1997). Even so, during the 1993 outbreak in France, most nests were in marshes or humid areas and only 10% of pairs nested in crops (Michelat 1997). In Spain, 55% of 76 pairs monitored nested in agricultural fields (of which 20 were in cereal crops), and some nests were even found in ploughed fields without vegetation cover (Jubete et al. 1996). In our study, all pairs nested in agricultural fields, possibly due to the scarcity of alternative habitats.

Breeding inside crops potentially results in the destruction of many nests due to mowing and harvesting. For instance, in Spain, 43% of 39 nests failed and 53% of the failures were due to har-

vesting activities. The remainder were due to predation (Jubete et al. 1996). Similarly, 31% of young in our study had to be protected at the time of harvesting and 11–44% of nests would have failed without our intervention. The lack of natural habitat might be an important factor limiting the distribution and breeding success of the Short-eared Owls and may also explain why edge areas are suboptimal except in occasional circumstances when prey abundance is particularly high.

Nest Spacing, Territoriality and Habitat Selection. Short-eared Owls are believed to be strongly territorial, establishing and maintaining territories through intraspecific agonistic behavior (Lockie 1955, Holt and Leasure 1993). Hunting takes place within the defended territory, and consequently, territory size depends on prey abundance (Lockie 1955, Clark 1975, Village 1987). Territory size is highly variable ranging from 15–200 ha in Europe (Mikkola 1983) and 20–126 ha in North America (Holt and Leasure 1993). In areas where owls do not hunt microtines, they hunt far away from nests (Lawton and Bowman 1986) and hunting ranges are as big as 286 ha in southern Chile, where birds also form an important part of Short-eared Owl diets (Martínez et al. 1998). Territory sizes and between-nest distances are particularly small in areas and years with vole superabundance (Village 1987).

In our study, distribution of nests did not match that of a typical territorial raptor, and nests were clumped similar to raptors that use open habitats such as harriers (Krogulec and Leroux 1993, Arroyo 1995). Only Holt and Leasure (1993) describe Short-eared Owls as facultatively breeding in loose colonies in North America. Such clumped distribution might result from the clumping of voles. This is possible, given that Short-eared Owls in our study nested in the area where voles were most abundant and crops with high vole abundance were selected. However, the association with harriers that we observed may indicate that other factors influence the choice of nest sites, given that harriers usually hunt far away from the nests (Salamolard 1997). Associations between Short-eared Owls and harriers have also been described by Urner (1925) and in the Buena Vista Marsh (Beske and Champion 1971), where all of the 17 owl territories overlapped with harrier territories. The aggregation of Short-eared Owl nests and association with harriers may be related to predator detection and defense, as predation has been shown to be

an important factor explaining Short-eared Owl breeding success in other areas (Lockie 1955). Similarly, the rapid rate of growth shown by Short-eared Owl young and their early dispersal from nests is also likely related to predator avoidance. Holt et al. (1992) found that the most rapid weight increase in Short-eared Owls occurred between 11–15 d and coincided with pre fledging dispersal from nests which takes place at about 14–17 d (Holt and Leasure 1993). We found a slightly earlier pre fledging dispersal and that dispersal distances were higher than those previously reported (55 m in Holt and Leasure 1993). These differences may have been due to habitat characteristics related to vegetation density and predation risk between crops and natural habitats, although more data are needed to verify the latter.

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LITERATURE CITED

- ARROYO, B.E. 1995. Breeding ecology and nest dispersion in the Montagu's Harrier *Circus pygargus* in central Spain. Ph.D. dissertation, Oxford Univ., Oxford, U.K.
- ASENSIO, B., F. CANTOS, A. FERNANDEZ AND I. FAJARDO 1992. La lechuza campestre en España. *Quercus* 1992:18–24.
- BESKE, A. AND J. CHAMPION. 1971. Prolific nesting of Short-eared Owls on Buena Vista marsh. *Passenger Pigeon* 33:99–103.
- BUTET, A. AND A. LEROUX. 1993. Effect of prey on a predator's breeding success. A 7-year study on common vole (*Microtus arvalis*) and Montagu's Harrier (*Circus pygargus*) in a west of France marsh. *Acta Oecol.* 14:857–865.
- CLARK, P.J. AND F.C. EVANS. 1954. Distance to nearest neighbor as a measure of spatial relationships in populations. *Ecology* 35:445–453.
- CLARK, R.J. 1975. A field study of the Short-eared Owl, *Asio flammeus* (Pontoppidan), in North America. *Wildl. Monogr.* 47:1–67.
- CRAMP, S. [ED.]. 1985. The birds of the western Palearctic. Vol. 4. Oxford Univ. Press, Oxford, U.K.
- DELATTRE, P., P. GIRAUDOUX, J. BAUDRY, D. TRUCHETET, P. MUSARD, M. TOUSSAINT, P. STAHL, M.L. POULE, M. ARTOIS, J.P. DAMANGE AND J.P. QUÉRÉ. 1992. Land use patterns and types of common vole (*Microtus arvalis*)

- population kinetics. *Agric. Ecosyst. & Environ.* 39:153–169.
- GRÖNDLUND, S. AND H. MIKKOLA. 1969. On the ecology of the Short-eared Owl in Lapua Alajoki in 1969. *Suomenselan Linnut* 4:68–76.
- HOLT, D.W. 1992. Notes on Short-eared Owl, *Asio flammeus*, nest sites, reproduction, and territory sizes in coastal Massachusetts. *Can. Field-Nat.* 106:352–356.
- . 1993. Trophic niche of nearctic Short-eared Owls. *Wilson Bull.* 105:497–503.
- AND S.M. LEASURE. 1993. Short-eared Owl. In A. Poole and F. Gill [Eds.], *The birds of North America*, No. 62. The Academy of Natural Sciences, Philadelphia, PA and the American Ornithologists' Union, Washington, DC U.S.A.
- , M. MELVIN AND B. STEELE. 1992. Nestling growth rates of Short-eared Owls. *Wilson Bull.* 104:326–333.
- HOLZINGER, J., M. MICKLEY AND K. SCHILHAUSL. 1973. Untersuchungen zur Brut- und ernährungsbiologie der Sumpfohreule (*Asio flammeus*) in einem süddeutschen Brutgebiet mit bemerkungen zum auftreten der art in Mitteleuropa. *Anz. Ornithol. Ges. Bayern* 12:176–197.
- JUBETE, F., A. ONRUBIA AND J. ROMÁN. 1996. La lechuza campestre en España: de invernante a reproductor. *Quercus* 1996:19–22.
- KORPIMÄKI, E. 1984. Population dynamics of birds of prey in relation to fluctuations in small mammal populations in western Finland. *Ann. Zool. Fenn.* 21:287–293.
- AND K. NORRDAHL. 1991. Numerical and functional responses of kestrels, Short-eared Owls and Long-eared Owls to vole densities. *Ecology* 72:814–826.
- KREBS, C. 1989. *Ecological methodology*. Harper and Row, New York, NY U.S.A.
- KROGULEC, J. AND A. LEROUX. 1993. Breeding ecology of Montagu's Harrier *Circus pygargus* on natural and reclaimed marshes in Poland and France. In B.-U. Meyburg and R.D. Chancellor [Eds.], *Raptor conservation today*. Pica Press, Cornwall, U.K.
- LAWTON, J. AND N. BOWMAN. 1986. Diet and ecology of Short-eared Owls *Asio flammeus* breeding on heather moor. *Bird Study* 33:12–17.
- LOCKIE, J.D. 1955. The breeding habits and food of Short-eared Owls after a vole plague. *Bird Study* 2:63–69.
- MARTÍNEZ, D.R., R.A. FIGUEROA, C.L. OCAMPO AND F.M. JAKSIC. 1998. Food habits and hunting ranges of Short-eared Owls (*Asio flammeus*) in agricultural landscapes of southern Chile. *J. Raptor Res.* 32:111–115.
- MICHELAT, D. 1997. La nidification du Hibou des marais *Asio flammeus* en France en 1993. *Ornithos* 4:35–40.
- MIKKOLA, H. 1983. *Owls of Europe*. T & A.D. Poyser Ltd, Calton, U.K.
- NEU, C.W., C. RANDALL BYERS AND J.M. PEEK. 1974. A technique for analysis of utilization-availability data. *J. Wildl. Manage.* 38:541–545.
- RAU, J.R., M.C. VILLAGRA, M.L. MORA, D.R. MARTÍNEZ AND M.S. TILLERIA. 1992. Food habits of the Short-eared Owl (*Asio flammeus*) in southern South America. *J. Raptor Res.* 26:35–36.
- SALAMOLARD, M. 1997. Utilisation de l'espace par le Busard cendré *Circus pygargus*. Superficie et distribution des zones de chasse. *Alauda* 65:307–320.
- SPITZ, F. 1977. Développement d'un modèle de prévision des pullulations du campagnol des champs. *Bull. OEPP* 7:341–347.
- , H. LE LOUARN, A. POULET AND B. DASSONVILLE. 1974. Standardisation des piégeages en ligne pour quelques espèces de rongeurs. *Terre Vie* 28:564–578.
- URNER, C.A. 1925. Notes on two ground-nesting birds of prey. *Auk* 42:31–41.
- VILLAGE, A. 1987. Numbers, territory size and turnover of Short-eared Owls *Asio flammeus* in relation to vole abundance. *Ornis Scand.* 18:198–204.
- WIEBE, K.L. 1991. Food habits of breeding Short-eared Owls in southwestern British Columbia. *J. Raptor Res.* 25:143–145.
- YEATMAN-BERTHELOT, D. AND G. JARRY. 1991. *Atlas des oiseaux de France en hiver*. S.O.F., Paris, France.
- . 1994. *Nouvel atlas des oiseaux nicheurs*. S.O.F., Paris, France.

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POPULATION TREND OF ADULT BALD EAGLES IN SOUTHEAST ALASKA, 1967–97

MICHAEL J. JACOBSON AND JOHN I. HODGES

U.S. Fish and Wildlife Service, 3000 Vintage Boulevard, Suite 240, Juneau, AK 99801-7100 U.S.A.

ABSTRACT.—Six aerial surveys to estimate the population size of adult Bald Eagles (*Haliaeetus leucocephalus*) in southeast Alaska were conducted from 1967–97. A stratified random sampling method was used, focusing on plots 166 km² in size. All surveys were flown in late April and early May when egg laying and early incubation were in progress. A fitted regression line ($P = 0.02$) indicated the adult Bald Eagle population increased 92% during the survey period, from 6941 in 1967 to 13 327 in 1997. However, we detected no significant population differences from 1982–97, which suggested the population may have begun to stabilize. The increase of the adult Bald Eagle population in southeast Alaska probably represents a recovery from the effects of the 1917–53 eagle bounty in Alaska when as many as 150 000 Bald Eagles were killed. The later establishment of protection zones at eagle nest trees and other key waterfront habitat on national forest lands (80% of the land base) may have helped allow the population to increase.

KEY WORDS: *Bald Eagle, Haliaeetus leucocephalus; southeast Alaska; population trend; aerial surveys; random plot sampling.*

Tendencia poblacional de las águilas calvas en el sureste de Alaska, 1967–97

RESUMEN.—Seis monitoreos aéreos para estimar el tamaño de la población fueron llevados a cabo en Alaska entre 1967–97. Un método de muestreo estratificado al azar fué utilizado mediante parcelas de 166 km² de tamaño. Todos los vuelos fueron realizados hacia finales de Abril y principios de Mayo durante la época de anidación e incubación. Una regresión lineal ($P = 0.02$) indicó que la población se incrementó en un 92% durante el período de investigación de 6941 en 1967 a 13 327 en 1997. Sin embargo no detectamos ninguna diferencia poblacional significativa entre 1982–97, lo que sugiere que quizás la población ha comenzado a estabilizarse. El incremento en la población adulta en el sureste de Alaska probablemente representa una recuperación de los efectos de incentivos de caza entre 1917–53, en donde 150 000 águilas calvas fueron eliminadas. El reciente establecimiento de medidas de protección en las zonas de árboles de anidación y en habitats acuáticos en tierras de bosques nacionales (80% de estos) probablemente ha permitido el incremento de la población.

[Traducción de César Márquez]

Bald Eagles (*Haliaeetus leucocephalus*) are at their greatest abundance along the northern Pacific coast of North America, reaching highest densities in southeast Alaska, Prince William Sound and coastal British Columbia (King et al. 1972, Hodges et al. 1979, 1984, Bowman et al. 1995, 1997). The first aerial survey to provide an estimate of the adult Bald Eagle population in southeast Alaska was conducted in 1967. We completed the sixth comparable survey in 1997. With roughly 24 000 km of coastal shoreline in southeast Alaska, an aerial survey of the total shoreline was not practical. Stratified random sampling provided an accurate and repeatable method to estimate the numbers of adult bald eagles present in the breeding season.

METHODS

King et al. (1972) divided the entire coastline of southeast Alaska into 488 plots, each 166 km². From these, 30 plots were chosen at random, and each plot was classified into one of three strata (low, medium, high) based on the complexity of shoreline habitat within the plot and the expected density of eagles (Hodges et al. 1979, 1984). The stratified random sample of 30 plots was then used to extrapolate numbers of adult Bald Eagles for all of southeast Alaska. The same 30 plots have been surveyed six times by fixed-wing aircraft over a span of 30 yr: 1967, 1977, 1982, 1987, 1992 and 1997 (Fig. 1).

Adult Bald Eagles, with their large size and distinct white heads and tails, contrasted well against the dark spruce-hemlock coastal forest found in southeast Alaska. Perched immature eagles, with dark plumage; were difficult to see and, thus, we expected to observe a low percentage of them. However, since 1982, we have tried to estimate the percentage of immature eagles in the pop-

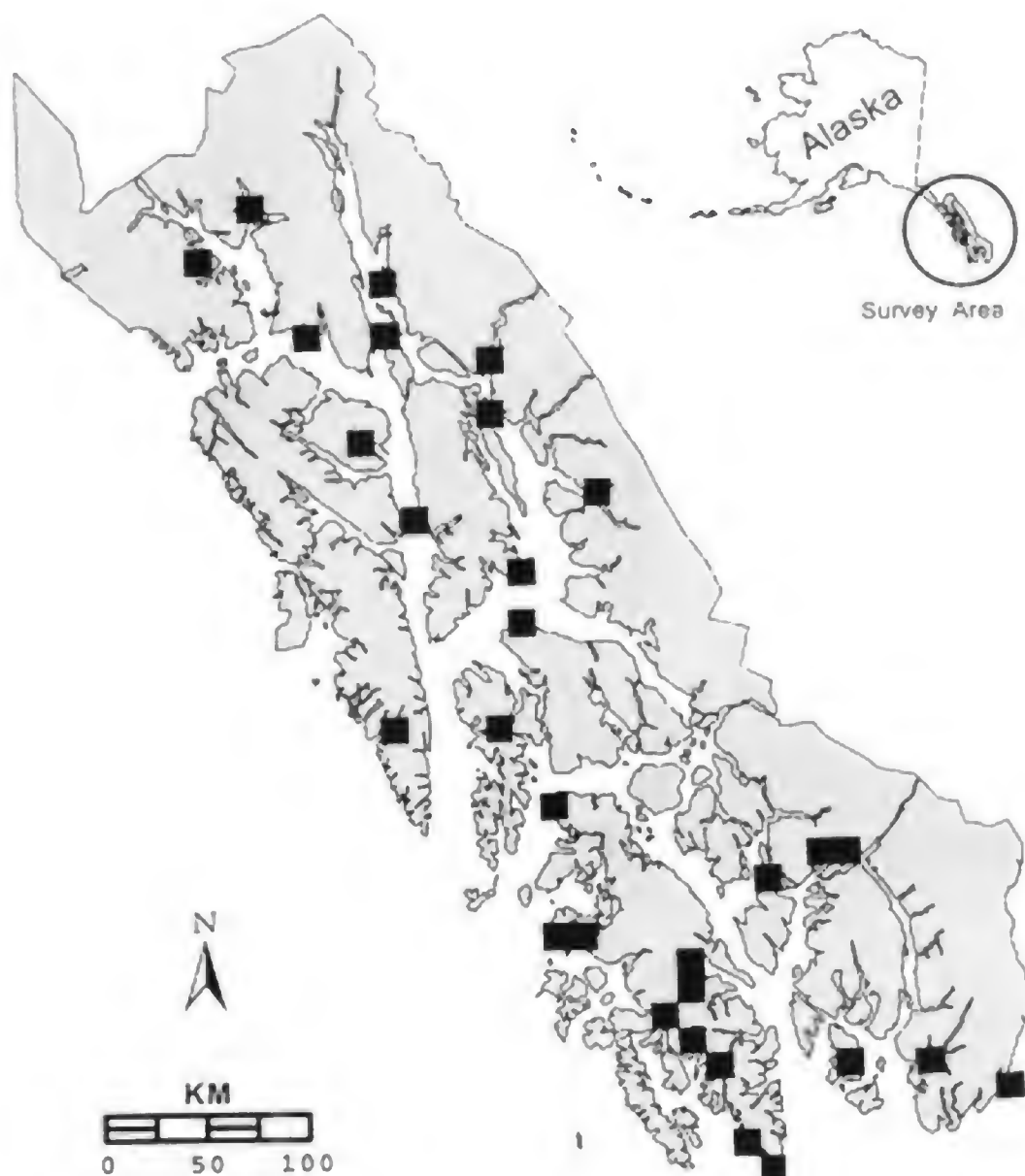


Figure 1. Location of 30 randomly selected plots surveyed for Bald Eagles in southeast Alaska in 1967, 1977, 1982, 1987, 1992 and 1997. These plots were used to estimate the population size of adult eagles in all of southeast Alaska.

ulation by recording the proportion of immature and adult eagles observed flying (Bowman et al. 1997, Hodges et al. 1984). Assuming all ages were equally visible while they were flying, and all ages were as likely to be flying, the proportion of flying immatures to flying adults provided an estimate of the percentage of immature birds in the population.

A turbine DeHavilland Beaver aircraft on amphibious floats was flown for every survey except 1967 when a Cessna 180 was used. Surveys were flown at an average altitude of 90 m and airspeed of 160 km/hr. All surveys were conducted in late April and early May when many adult eagles were near nest sites. Egg laying by Bald Eagles in southeast Alaska usually takes place during mid- to late-April, with hatching in late May and early June (U.S. Fish and Wildl. Serv., unpubl. data). Total flight hours for the six surveys varied from 32.0–37.8, with differences attributed to changing transit times. The observer and pilot both searched for eagles and the observer recorded observations directly onto 1:63 360 scale U.S. Geological Survey maps. The aircraft was flown along shorelines in a direction to provide optimum visibility for the observer in the right front seat.

Statistical procedures included stratified random sample, simple linear regression, and paired *t*-test (Snedecor

and Cochran 1967). Confidence limits on estimates of the percentage of all flying eagles that were immatures were calculated assuming independence and a binomial distribution (Fowler and Cohen 1986).

RESULTS

A simple linear regression of the six survey points from 1967–97 indicated the adult Bald Eagle population in southeast Alaska increased an estimated 92% during that period (Fig. 2). The regression line placed the adult population at 6941 in 1967. The 1997 predicted value of $13\,327 \pm 2592$ (95% confidence limits) equated to 0.55 adults per km of shoreline. Actual individual population estimates increased from 7230 adult eagles in 1967 to 12 026 eagles in 1997 (Table 1). A paired *t*-test, using plots as sample units, failed to detect significant population differences between the 1982–97 surveys. From 1982–97, immature eagles averaged $13.3\% \pm 4.7\%$ of all eagles seen flying (Table 2).

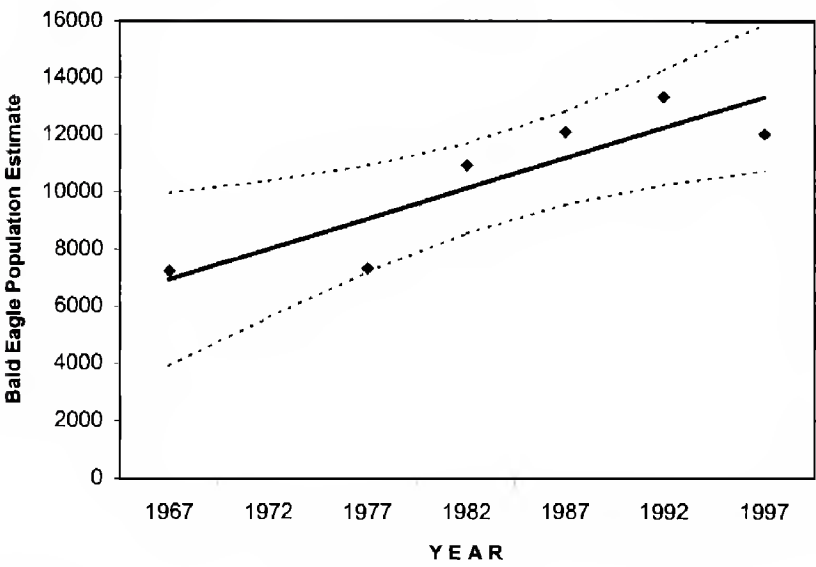


Figure 2. Population estimates calculated from aerial surveys of adult Bald Eagles in southeast Alaska in 1967–97. The solid line indicates the fitted regression line ($P = 0.02$) and the 95% confidence limits are shown as dashed lines.

DISCUSSION

Our surveys proved to be a feasible way of monitoring the trend in the Alaskan Bald Eagle population over a broad area. The increase in the adult segment of the Bald Eagle population in southeast Alaska probably represented a recovery from the effects of the eagle bounty which occurred between 1917–53. Bounties were offered on the erroneous assumption that eagles seriously impacted the salmon and fur industries. During that period, as many as 150 000 Bald Eagles were killed in Alaska, with the majority coming from the southeast region (King et al. 1972). Hansen and Hodges (1985) suggested that the eagle population was greatly reduced during the bounty period and may have rebounded since that time. Although our data have shown a dramatic increase in the Bald Eagle population since 1967, the estimated decline in 1997 possibly indicated that the population has begun to stabilize.

The estimated population totals are minimum estimates since some adult eagles were undoubtedly missed during surveys. Bowman et al. (1993) developed an estimate of visibility bias for Bald Eagles in Alaska’s Prince William Sound, an area of coastal habitat similar to that found in southeast Alaska. Using radio-tagged Bald Eagles, they estimated that they would have seen an adult eagle in 68% of observations during a typical population survey. Applying this correction factor to the regression line prediction for 1997 would give a pop-

Table 1. Population estimates of adult Bald Eagles in southeast Alaska during spring of 1967, 1977, 1982, 1987, 1992 and 1997. Stratified random sampling was used, all plots were 166 km² in size.

YEAR	POPULATION ESTIMATE	STANDARD ERROR of ESTIMATE
1967	7230	458
1977	7329	457
1982	10 934	1606
1987	12 075	1219
1992	13 340	1185
1997	12 026	1554

ulation of 19 599 adult Bald Eagles in southeast Alaska.

In southeast Alaska, the proportion of flying immatures to flying adults was lower than reported in other coastal areas. Bowman et al. (1997) found immatures comprised 29.2% of all eagles seen flying during similar population surveys at Prince William Sound in 1982, 1989, 1990, 1991 and 1995. Hodges et al. (1984) reported immatures were 27% of all flying eagles during a 1980 survey of coastal British Columbia. More emphasis on the development of visibility correction factors could improve future estimates of adult and immature eagle numbers in southeast Alaska.

Eagles were widely distributed throughout the study area during all surveys. It is possible that eagles concentrating at feeding areas could have influenced our data; however, we rarely encountered this situation. On most surveys, we attempted to search for possible feeding concentrations outside the plots, but did not find large enough numbers of eagles to suggest the possibility of a substantial bias in our estimates.

Industrial scale clearcut logging began in south-

Table 2. Age ratios of Bald Eagles seen flying during population surveys in southeast Alaska in 1982, 1987, 1992 and 1997.

YEAR	No. IM-MATURES	No. ADULTS	% IM-MATURES	±95% CI
1982	4	58	6.5	6.2
1987	12	58	17.1	9
1992	8	37	17.8	11.4
1997	4	30	11.8	11
All years	28	183	13.3	4.7

east Alaska at about the same time the eagle bounty ended. Early logging practices sometimes included the removal of easily attainable old-growth timber along the waterfront, the same area where most eagles are found (Hodges and Robards 1982). Since 1968, a cooperative agreement between the U.S. Fish and Wildlife Service and the U.S. Forest Service (USFS) has provided for a protection zone of 100 m radius around each Bald Eagle nest tree identified on national forest lands (80% of the land base) in southeast Alaska. Later changes to the agreement added protection of eagle perching and roosting habitat. The USFS now restricts most timber harvest within 300 m of the beach (USDA Forest Service 1997). Logging practices on private lands (10% of the land base) have been less restrictive and, therefore, less successful in retaining nest tree buffer zones and protecting other key waterfront habitat for eagles. Nevertheless, protective measures across the majority of southeast Alaska may have helped allow the Bald Eagle population to increase since the elimination of the bounty.

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LITERATURE CITED

BOWMAN, T.D., P.F. SCHEMPF AND J.A. BERNATOWICZ. 1993. Effects of the Exxon Valdez oil spill on Bald Eagles.

- Exxon Valdez Oil Spill State and Fed. Nat. Resour. Damage Assess. Final Rep., Bird Stud. 4. U.S. Fish and Wildl. Serv., Anchorage, AK U.S.A.
- , ——— AND ———. 1995. Bald Eagle survival and population dynamics in Alaska after the Exxon Valdez oil spill. *J. Wildl. Manage.* 59:317–324.
- , ——— AND J.I. HODGES. 1997. Bald Eagle population in Prince William Sound after the Exxon Valdez oil spill. *J. Wildl. Manage.* 61:962–967.
- FOWLER, J. AND L. COHEN. 1986. Statistics for ornithologists. Br. Trust Ornithol. Guide 22, London, U.K.
- HANSEN, A.J. AND J.I. HODGES. 1985. High rates of non-breeding adult Bald Eagles in southeastern Alaska. *J. Wildl. Manage.* 49:454–458.
- HODGES, J.I. AND F.C. ROBARDS. 1982. Observations of 3,850 Bald Eagle nests in southeast Alaska. Pages 37–46 in W.N. Ladd and P.F. Schempf [EDS.], Raptor management and biology in Alaska and western Canada. FWS/AK/PROC-82, U.S. Fish and Wildl. Serv., Anchorage, AK U.S.A.
- , J.G. KING AND F.C. ROBARDS. 1979. Resurvey of the Bald Eagle breeding population in southeast Alaska. *J. Wildl. Manage.* 43:219–221.
- , ——— AND R. DAVIES. 1984. Bald Eagle breeding population survey of coastal British Columbia. *J. Wildl. Manage.* 48:993–998.
- KING, J.G., F.C. ROBARDS AND C.J. LENSINK. 1972. Census of the Bald Eagle breeding population in southeast Alaska. *J. Wildl. Manage.* 36:1292–1295.
- SNEDECOR, G.W. AND W.G. COCHRAN. 1967. Statistical methods. 6th Ed. Iowa State Univ. Press, Ames, IA U.S.A.
- USDA FOREST SERVICE. 1997. Tongass land management plan and final environmental impact statement. Ser No. R10-MB-338b., part 1, chap. 3. USDA For. Serv., Alaska Region, Juneau, AK U.S.A.

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DETECTION OF BALD EAGLES DURING AERIAL SURVEYS IN PRINCE WILLIAM SOUND, ALASKA

TIMOTHY D. BOWMAN

U.S. Fish and Wildlife Service, 1011 East Tudor Road, Anchorage, AK 99503 U.S.A.

PHILIP F. SCHEMPF

U.S. Fish and Wildlife Service, 3000 Vintage Boulevard, Juneau, AK 99801 U.S.A.

ABSTRACT.—Bald Eagles (*Haliaeetus leucocephalus*) are often counted by aerial surveys but, because some birds are not detected, this approach provides only an index to population size. We estimated detection rates for Bald Eagles during fixed-wing aerial surveys in Prince William Sound, Alaska to extrapolate the index to an estimate of the total population of Bald Eagles in Prince William Sound. Using a modified Petersen estimate and independent front and back seat observers, we estimated that we detected 79% and 51% of observable adult and immature eagles, respectively. Using data from a radio-telemetry study, we also estimated that 21% of adult eagles were unavailable for detection because they were in locations not visible to airborne observers following the shoreline at tree-top level. Combining both perception and availability biases, 62% of adult eagles was seen (visibility correction factor of 1.6). Detection rates were similar between a Cessna 185 and a turbine DeHavilland Beaver aircraft. We believe these detection rates are generally applicable to Bald Eagles in the coniferous coastal forests from Washington to Alaska, but encourage collection of similar data in future surveys to enable estimates of site-specific detection rates.

KEY WORDS: *Bald Eagle, Haliaeetus leucocephalus; aerial survey; detection rates; visibility bias; Prince William Sound, Alaska.*

Detección de águilas calvas durante los monitoreos aéreos en Prince William Sound, Alaska

RESUMEN.—Las águilas calvas (*Haliaeetus leucocephalus*) son usualmente contadas en monitoreos aéreos, debido a que algunos individuos no son detectados, este enfoque provee tan sólo un índice del tamaño poblacional. Estimamos las tasas de detección de águilas calvas durante monitoreos aéreos en Prince William Sound. Utilizamos un estimativo modificado de Petersen con observadores independientes adelante y atrás, estimamos que detectamos 79% y 51% de los adultos observables y de los juveniles respectivamente. Mediante la utilización de datos y de un estudio de telemetría, estimamos también que el 21 % de las águilas adultas no pudieron ser detectadas debido a que se encontraban en sitios no visibles a los observadores al seguir la línea de costa y el dosel de los árboles. Al combinar ambos, los sesgos de percepción y disponibilidad, 62% de las águilas fueron detectadas (factor de corrección de visibilidad de 1.6). Las tasas de detección fueron similares entre un Cessna 185 y un avión DeHavilland Beaver de turbina. Creemos que las tasas de detección son en general aplicables a las águilas calvas en los bosques de coníferas costeras desde Washington a Alaska, pero recomendamos la recolección de datos similares en monitoreos futuros con el fin de estimar tasas de detección en sitios específicos.

[Traducción de César Márquez]

Bald Eagle (*Haliaeetus leucocephalus*) populations are often censused using aerial surveys (King et al. 1972, Hodges et al. 1984, Fuller and Mosher 1987). Adult Bald Eagles have conspicuous white heads and tails and typically perch in prominent positions where they are easily seen. Immature eagles have less conspicuous plumage, select less prominent perch sites (Hancock 1964) and are relatively

difficult to see or accurately count during aerial surveys. Because some eagles are missed or impossible to see, population surveys provide indexes that represent a constant but unknown fraction of the total population. Indices are seldom free of visibility bias and usually underestimate true population size. Although indices are usually adequate for monitoring population trends, estimates of total

population size are sometimes needed for modeling population dynamics, estimating the probability of extinction, or evaluating the effects of catastrophic events. Survey-specific visibility correction factors can help standardize for biases that vary among surveys or over time, and enable better comparisons of numbers among populations with different detection rates or that are surveyed using different methods. Consequently, visibility-adjusted indexes can, in some instances, facilitate and improve management decisions.

The detectability of animals to airborne observers may be influenced by environmental conditions (e.g., time of day, weather, snow cover, topography, season, habitat), observers (e.g., level of ability, experience, fatigue), aircraft factors (e.g., type of aircraft, speed, altitude, window size and position) and biological factors (e.g., animal behavior, age and sex of animal, breeding status) (King et al. 1972, Grier 1977, Leighton et al. 1979, Grier et al. 1981, Hodges and King 1982, Kochert 1986, Fuller and Mosher 1987, Pollock and Kendall 1987). Marsh and Sinclair (1989) described two categories of missed animals: those that are potentially available to observers but are not seen (perception bias) and those that are not available to observers because they are concealed by vegetation, other animals, turbid water, topographic features, or temporarily absent (availability bias).

Using data from a range of wildlife surveys, Caughley (1977) showed that 30–60% of animals are often missed. Estimates of detectability of eagles are generally lacking, but, based on a combination of quantitative and qualitative methods, Hancock (1964) concluded that adult Bald Eagles can be undercounted by <10–15% and immatures by 20–35% during winter aerial surveys in coastal British Columbia. Buehler et al. (1991), on Chesapeake Bay, Maryland, estimated that they saw 31–75% of detectable eagles and that 31–49% were off aerial survey routes when flown throughout the year. Hodges (pers. comm.) recommended using a correction factor of 2.5 when estimating number of eagles missed by observers, based on simulations with hypothetical detection probability distributions.

In this study, we used a two-sample capture-recapture (Lincoln-Petersen) estimator (Seber 1973, Magnussen et al. 1978) using two independent observers recording simultaneously to estimate detection rate of eagles in Prince William Sound, Alaska. The paired observer method estimated only per-

ception bias and did not account for availability bias (eagles with zero probability of being seen, such as those perched in areas off the survey route or birds soaring at high altitude). We estimated availability bias using a sample of radio-tagged adult eagles (Bowman et al. 1993) and combined it with estimates of perception bias to estimate an overall visibility correction factor.

STUDY AREA

Prince William Sound is located in southcentral Alaska and encompasses about 39 000 km² including 4800 km of shoreline. The coastline is complex with many islands, particularly in the western Sound. Temperate rainforest dominated by Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*) grows to an elevation of about 500 m. It is relatively uniform in species composition but varies in structure, density, interspersions of forest and clearings and age. The area we surveyed included all islands in Prince William Sound and randomly selected plots on mainland areas. Only shorelines were searched; we did not survey river valleys or inland areas. Snow was present on the ground in some areas when we surveyed.

There are about 6000 eagles in Prince William Sound, with nest densities as high as 0.5/km of shoreline (Bowman et al. 1997). Bald Eagles nest exclusively in trees in Prince William Sound and incubation begins in mid- to late-April. As is typical of coastal nesting Bald Eagles (Hancock 1964, Hodges and Robards 1982), nearly all nests were <200 m of the shoreline.

METHODS

The survey was intended to provide an index of the resident adult eagle population, and therefore was flown early in the nesting period presumably when migrant eagles had left the area for their respective breeding areas (e.g., along inland rivers) and movements of local breeders were limited by nesting activity. We used Cessna 185 and turbine DeHavilland Beaver aircraft on amphibious floats. Survey methodology followed Hodges et al (1984).

We searched shorelines from an altitude of 50–100 m at an airspeed of about 160 km/hr, with most shorelines (and eagles) on the right side of the aircraft. The front right seat observer recorded his and the pilot's observations from either side of the aircraft on continuously-running cassette tapes and on USGS 1:63 360 scale topographic maps. The back seat observer counted eagles only on the right side of the aircraft, and simultaneously recorded observations on cassette tapes. The back seat observer was audibly (headsets) and visually (barrier) separated from the front seat observers. We recorded observations for 3–15 min periods and synchronized our cassette recordings. We noted general weather conditions encountered during each recording session.

We spent one day flying before we began our survey to develop our search image and to refine the protocol for recording observations on tape. We did not use data from that day in this analysis.

Tapes were transcribed using a computer data entry

program (Butler et al. 1995) to determine the time from the start of each recording period for each observation (as determined by the proportion of elapsed time from start of transect). We matched right side observations made by the front and rear seat observers using the category designation (age, behavior and relative sightability), time elapsed from the start of the recording session and observers' descriptions of eagles (e.g., distance from shore, elevation, type of tree, position in tree). Left side observations were excluded because they were not available to the back seat observer.

The percentage of birds seen by front seat observers (perception bias) was estimated by:

$$\frac{n_2}{N} = \frac{m_2}{n_1}$$

where, N = total number of eagles visible (population size), n_1 = number of eagles seen by back seat observer (marked sample), n_2 = number seen by front seat observers (recaptured sample), m_2 = number seen by both the back and front seat observers (number in recaptured sample that were marked).

Estimates of detectability applied to the combined efforts of pilots and front seat observer because front seat observer and pilots combined sightings. Variance of the estimate was calculated for a proportion with binomial distribution according to Fowler and Cohen (1986).

Assumptions of the Petersen estimator are that sightings of different objects by different observers occur independently, the population is constant in size during the observation period, there are no errors in determining which objects are seen by either one, or both, of the observers, and each object has the same probability of being seen by any one observer (although observers may differ in their detection such as when one observer's window affords a better view than the other's). We probably met the first assumption because observers were effectively audibly and visually isolated from each other and, for the most part, eagles were sparsely distributed and sightings occurred independently (although paired eagles perched nearby one another may have influenced detection of their mate). The population was constant in size because observations by the two observers were made simultaneously. We are confident that we reasonably met the third assumption because most adult eagles occupied territories, often with considerable distances between them, and because we made notes on behavior or location that aided us in matching observations. We recognized that eagles were likely to have different sighting probabilities related to their behavior, location, plumage and habitat use so we addressed the assumption of equal probability of detection by dividing the population of eagles into subsets with relatively similar detectability. We estimated detection rates independently for each subset but did not report detection rates for categories with fewer than seven matched observations because estimates can be biased with <7 matched observations (Seber 1973).

A weighted average detection for the subdivided population of adult eagles was calculated as:

$$p = \frac{\sum n_{2i}}{\sum \hat{N}_i}$$

We used the following categories for observations: (1) adult perched, easy to see; (2) adult perched, moderately difficult to see, (3) adult perched, very difficult to see; (4) adult flying (below wing level); (5) adult soaring (above wing level); (6) adult incubating; (7) immature perched; and (8) immature flying. These categories were intended to subset the population into groups with relatively similar detectability. Although we recorded three categories of perched adults (easy, moderate and very difficult), there was enough subjectivity in these categories that, to facilitate matching, we reduced it to two categories. If either observer called a matched bird easy to see, it was tallied in the easy category. All other combinations of categories (e.g., moderate/difficult, moderate/moderate, difficult/difficult) were included in the difficult category.

We estimated availability bias by observing 38 radio-tagged adult eagles during the incubation period (timing similar to population surveys), which we relocated from fixed-wing aircraft in 1990–91. When we visually observed a radio-tagged eagle, we noted bird activity (e.g., soaring, perched, incubating) and location (e.g., tree, beach, elevation or altitude), and noted whether the eagle, for whatever reason, would have been impossible to see (i.e., availability bias) during a typical population survey focused primarily on shoreline habitats at lower elevations. Radio-tagged eagles included both males and females; all were believed to be breeding birds. Standard error of the estimated proportion impossible to see was estimated for a proportion with binomial distribution according to Fowler and Cohen (1986).

We also recorded weather conditions during telemetry flights, noting the extent and height of cloud cover and the presence of fog or rain. The range of weather conditions encountered during telemetry flights was similar to weather conditions during population surveys. Ramy or windy days were avoided while surveying because flying conditions are impossible or unsafe.

RESULTS

Detection of eagles was similar from both aircraft when flown under similar weather conditions (Table 1). Therefore, we pooled data for both planes. Detection rates varied among subsets. Perched adults (detectability perched easy = 0.935, SE = 0.01; detectability perched difficult = 0.561, SE = 0.05) were more likely to be seen than perched immatures (0.419, SE = 0.09), but detectability of flying adults (0.815, SE = 0.07) was similar to flying immatures (0.833, SE = 0.11). The overall weighted perception bias (perched + flying) was 0.790 (SE = 0.018) for adult eagles and 0.512 (SE = 0.036) for immature eagles. Perception bias using an uncategorized approach (i.e., pooling categories only by age) was 0.85 for adults and 0.54 for immatures.

Of 38 radio-tagged adult eagles located during the incubation period, we estimated 21% (8 of 38) were impossible to see because they were soaring

Table 1. Detection probabilities of Bald Eagles during aerial surveys in Prince William Sound, Alaska, 1995.

DATE	AIRCRAFT	ENVIRONMENTAL CONDITIONS	DETECTION PROBABILITY (SE ^a) [n ^b]					
			ADULT		ADULT		ADULT	
			PERCHED, EASY	PERCHED, DIFFICULT	FLYING ^c	INCUBATING	PERCHED	FLYING ^c
21 April	Cessna 185	High overcast, calm	0.945 (0.020) [139]	0.667 (0.086) [48]	NA ^d	NA	NA	NA
23 April	Turbine Beaver	Cloudy/ broken skies, fog patches	0.968 (0.016) [135]	0.684 (0.075) [62]	0.778 (0.139) [16]	NA	0.615 (0.135) [14]	NA
26 April	Turbine Beaver	Sunny, calm	0.917 (0.022) [172]	0.500 (0.086) [56]	0.778 (0.139) [12]	NA	NA	NA
27 April	Turbine Beaver	Sunny, calm, extensive snow cover	0.891 (0.042) [65]	0.083 (0.080) [12]	NA	NA	NA	NA
All data pooled			0.935 (0.011) [511]	0.561 (0.047) [178]	0.815 (0.075) [41]	0.591 (0.105) [27]	0.419 (0.089) [30]	0.833 (0.108) [17]

^a Standard error.
^b Number of birds seen by front seat observers.
^c Indicates birds flying at or below aircraft wing level (i.e., not soaring at high altitude).
^d Insufficient number (<7) of matched observations to estimate detection.

high, perched somewhere not visible from a shoreline flight path, or incubating in a nest impossible to see from an aircraft.

Cumulative percent seen (perception bias * availability bias) was 0.623 (SE = 0.055). This was equivalent to a visibility correction factor of 1.6 (SE = 0.14) for adult eagles.

DISCUSSION

The 1995 index for Prince William Sound, which combined an island census and estimate from random plots on mainland, was 2641 adult eagles and an estimated 26.5% of the population (based on age ratios of flying eagles) were immatures (Bowman et al. 1997). Corrected for visibility, an estimated 4239 adult and 1528 immature (total of 5767) eagles resided in Prince William Sound in April 1995.

For most aerial surveys of Bald Eagles in Alaska and British Columbia, the age ratio of flying eagles has been used to represent the age ratio of eagles in the study area. This assumes that adults and immatures are equally likely to be flying (Hancock 1964, Hodges et al. 1984), although this assumption has never been tested. Using the age ratio of flying eagles, the proportion of immatures in the Prince William Sound population averaged 29% during 1989–95 surveys and did not vary significantly among years (Bowman et al. 1997). By adjusting counts for age-specific detection rates estimated during this survey, we estimated that only 8.4% of the population we surveyed were immatures. Therefore, our data suggested that immatures are more likely to be flying than adults, and that estimates based on age ratios of flying birds overestimated the proportion of immatures, and thus total population size. Intuitively, this seemed likely for several reasons. Many adults were incubating during the time of the survey and were less likely to be flying. Immatures may also have had different foraging strategies and flew more frequently to find adequate resources to survive (Gerrard and Bortolotti 1988).

Although inadequate number of replicates precluded a statistical assessment of specific factors influencing detection rates, we attributed the lower detection rates during the last two days of the survey to sunny weather as well as extensive snow cover encountered in mainland areas of western Prince William Sound on the last day of the survey. Throughout the survey, we had higher detectability under cloudy skies and reduced detectability under

sunny conditions. Under sunny skies, reflections and glare from the water and aircraft windows impaired visibility. Snow cover decreased contrast between white plumage and forest. Observer fatigue, due to cumulative effects of flying surveys several consecutive days, also could have been a confounding factor, although we believe it was insignificant relative to weather effects.

Our estimates of perception bias were similar to those made by Buehler et al. (1991) in Chesapeake Bay during the early nesting period (\bar{x} = 71.2% for January–March). Buehler et al. (1991) also estimated that about 40% of eagles were off survey routes and their estimated total correction factor (detectability and availability biases combined) of 2.38 was higher than ours (1.6) for the early nesting period. Hodges (pers. comm.) suggested a correction factor of 2.5 be applied to the number of missed (missed = estimated total population – number detected) observable eagles based on simulations with hypothetical detectability distributions. His result using simulations was roughly consistent with our empirical estimate of 0.79 detectability for adult eagles. Hodges found that the correction was robust to small variations in detectability distributions. Similarly, our empirical data comparing categorized and uncategorized estimates suggested that relative bias (bias/parameter) was 6–8%. Detection rates will be biased higher in populations with a high proportion of easily-detected animals versus a population with a high proportion of animals difficult to see (Seber 1973).

Our estimate for availability bias (i.e., that estimated using radio-tagged birds) was somewhat suspect because the sample of relocated eagles during the incubation period was small, we have no similar data for immature eagles, and radio-tagged adults included a disproportionate number of territorial birds, which were presumably more likely to be seen than nonterritorial eagles because they were associated with nest sites. Although our estimate gave an idea of the magnitude of availability bias in Prince William Sound, the applicability of our estimate to other areas warrants further investigation, and we encourage researchers with radio-tagged birds to estimate site specific and aircraft specific (e.g., fixed-wing vs. helicopter) detectability. Buehler et al.'s (1991) estimate of 40% off survey route is not directly comparable with our estimate of 21% due to differences in how the estimate was derived and because their sample in-

cluded a higher proportion of nonbreeding adults, which are more likely to range farther than territorial nesting birds. Nevertheless, their estimate and ours provide some insight into the magnitude of variation among areas. The proportion of eagles not observable certainly varies by geographic area because of differences in topography, climate, vegetation, food sources and between marine and inland areas.

Detection rates should apply to past surveys in forested areas of coastal Alaska because aircraft, techniques and observer skill were similar among surveys. Further, we believe these detection rates would be useful for surveys in similar habitats (e.g., coastal coniferous forests in northwestern North America) where detection rates are unknown and researchers wish to make some estimate of total population size from available indexes.

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LITERATURE CITED

- BOWMAN, T.D., P.F. SCHEMPF AND J.A. BERNATOWICZ. 1993. Effects of the Exxon Valdez oil spill on Bald Eagles. Exxon Valdez Oil Spill State and Fed. Nat. Resour. Damage Assess. Final Rep., Bird Stud. 4. U.S. Fish and Wildl. Serv., Anchorage, AK U.S.A.
- , ——— AND J.I. HODGES. 1997. Bald Eagle population in Prince William Sound after the Exxon Valdez oil spill. *J. Wildl. Manage.* 61:962–967.
- BUEHLER, D.A., T.J. MERSMANN, J.D. FRASER AND J.K.D. SEEGER. 1991. Differences in distribution of breeding, nonbreeding, and migrant Bald Eagles on the northern Chesapeake Bay. *Condor* 93:399–408.
- BUTLER, W.I., JR., J.I. HODGES AND R.A. STEHN. 1995. Locating waterfowl observations on aerial surveys. *Wildl. Soc. Bull.* 23:148–154.
- CAUGHLEY, G. 1977. Analysis of vertebrate populations. John Wiley & Sons, Inc., New York, NY U.S.A.
- FOWLER, J. AND L. COHEN. 1986. Statistics for ornithologists. Br. Trust Ornithol. Guide 22, London, U.K.
- FULLER, M.R. AND J.A. MOSHER. 1987. Raptor survey techniques. Pages 37–65 in B.A. Giron Pendleton, B.A. Millsap, K.W. Cline and D.M. Bird [Eds.], Raptor management techniques manual. Natl. Wildl. Fed., Washington, DC U.S.A.
- GERRARD, J.M. AND G.R. BORTOLOTTI. 1988. The Bald Eagle. Haunts and habits of a wilderness monarch. Smithsonian Inst. Press, Washington, DC U.S.A.
- GRIER, J.W. 1977. Quadrat sampling of a nesting population of Bald Eagles. *J. Wildl. Manage.* 41:438–443.
- , J.M. GERRARD, G.D. HAMILTON AND P.A. GRAY. 1981. Aerial-visibility bias and survey techniques for nesting Bald Eagles in northwestern Ontario. *J. Wildl. Manage.* 45:83–92.
- HANCOCK, D. 1964. Bald Eagles wintering in the southern Gulf Islands, British Columbia. *Wilson Bull.* 76:111–120.
- HODGES, J.I., JR. AND J.G. KING. 1982. Bald Eagle (Alaska) Pages 50–51 in D.E. Davis [Ed.], CRC handbook of census methods for terrestrial vertebrates. CRC Press, Boca Raton, FL U.S.A.
- AND F.C. ROBARDS. 1982. Observations of 3850 Bald Eagle nests in southeast Alaska. Pages 37–54 in W.N. Ladd and P.F. Schempf [Eds.], Raptor management and biology in Alaska and western Canada. U.S. Fish and Wildlife Service (FWS/AK/PROC-82), Anchorage, AK U.S.A.
- , J.G. KING AND R. DAVIES. 1984. Bald Eagle breeding population survey of coastal British Columbia. *J. Wildl. Manage.* 48:993–998.
- KING, J.G., F.C. ROBARDS AND C.J. LENSINK. 1972. Census of the Bald Eagle breeding population in southeast Alaska. *J. Wildl. Manage.* 36:1292–1295.
- KOCHERT, M.N. 1986. Raptors. Pages 313–349 in A.Y. Cooperrider, R.J. Boyd and H.R. Stuart [Eds.], Inventory and monitoring of wildlife habitat. USDI/BLM Service Center, Denver, CO U.S.A.
- LEIGHTON, F.A., J.M. GERRARD, P. GERRARD, D.W.A. WHITFIELD AND W. J. MAHER. 1979. An aerial census of Bald Eagles in Saskatchewan. *J. Wildl. Manage.* 43:61–69.
- MAGNUSSEN, W.E., G.J. CAUGHLEY AND G.C. GRIGG. 1978. A double-survey estimate of population size from incomplete counts. *J. Wildl. Manage.* 42:174–176.
- MARSH, H. AND D.F. SINCLAIR. 1989. Correcting for bias in strip transect aerial surveys of aquatic fauna. *J. Wildl. Manage.* 53:1017–1024.
- POLLOCK, K.H. AND W.L. KENDALL. 1987. Visibility bias in aerial surveys: a review of estimation procedures. *J. Wildl. Manage.* 51:502–509.
- SEBER, G.A.F. 1973. The estimation of animal abundance and related parameters. Charles Griffin and Company, London, U.K.

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ECOGEOGRAPHIC VARIATION IN MORPHOLOGY OF RED-TAILED HAWKS IN WESTERN NORTH AMERICA

BENJAMIN M. FITZPATRICK

Department of Biological Sciences, Humboldt State University, Arcata, CA 95521 U.S.A.

JEFFREY R. DUNK

Department of Wildlife and Department of Biological Sciences, Humboldt State University, Arcata, CA 95521 U.S.A.

ABSTRACT.—Geographic variation in external morphology of one subspecies of Red-tailed Hawk (*Buteo jamaicensis calurus*) in western North America was analyzed by comparing measurements of 249 museum specimens from seven ecoregions. Male and female Red-tailed Hawks showed substantial regional variation within the geographic range of this single subspecies. We used exploratory and confirmatory data analysis to investigate relationships between morphological and environmental variables. Canonical correlation indicated associations between morphology and continuous environmental variables. Five of six morphological measurements varied concordantly and were taken, collectively, to indicate size. In general, largest hawks occurred in the arid southwestern deserts and California grasslands, and smallest in the cool, humid Pacific Northwest. Tarsus length showed a pattern of variation opposite from other measurements, with longest tarsi in the Pacific Northwest. The traditional ecogeographic rules of Bergmann and Allen were not supported, nor did size appear to be related to availability of food. Our results were found to be consistent with some other ecomorphological hypotheses, such as James' "Neo-Bergmannian" hypothesis and those involving niche breadth, prey size and water conservation. Studies of the development, quantitative genetics and functional significance of size and shape are needed to understand the causes of ecogeographic variation.

KEY WORDS: *Red-tailed Hawk*; *Buteo jamaicensis*; *canonical correlation*; *geographic variation*; *morphometrics*; *biogeography*; *evolutionary ecology*.

Variación ecogeográfica en la morfología de *Buteo jamaicensis* en el oeste de Norteamérica

RESUMEN.—La variación geográfica en la morfología externa de una de las subespecies de gavilan cola roja (*Buteo jamaicensis calurus*) en el oeste de Norteamérica fué analizada al comparar las medidas de 249 especímenes de museo de siete ecoregiones. Machos y hembras mostraron una variación regional substancial dentro del rango geográfico de esta subespecie. Utilizamos el análisis de datos exploratorios para investigar las relaciones entre las variables morfológicas y ambientales. La correlación canónica indicó asociaciones entre la morfología y las variables ambientales continuas. Cinco o seis medidas morfológicas variaron en concordancia y fueron tomadas colectivamente para indicar tamaño. En general los gavilanes de mayor tamaño ocurrieron en los desiertos del suroeste y en los pastizales de California. Los más pequeños en la región húmeda y fría del noroeste pacífico. La longitud del tarso mostró un patrón de variación opuesto al de otras medidas con los tarsos mas largos en el noroeste Pacífico. Las reglas tradicionales de ecorregiones de Bergmann y Allen no fueron sustentadas como tampoco el tamaño estuvo relacionado con la disponibilidad de comida. Nuestros resultados fueron consistentes con otras hipótesis ecomorfológicas como la de James' "Neo-Bergmannian" y aquellas que involucran el tamaño del nicho, el tamaño de la presa y la conservación de las aguas. Los estudios relacionados con el desarrollo, la genética cuantitativa y el significado funcional del tamaño y la forma son necesarios para entender las causas de la variación ecogeográfica.

[Traducción de César Márquez]

Patterns of intraspecific variation are often viewed as key factors in understanding processes of adaptation and speciation (e.g., Darwin 1859, Wallace 1859, Power 1969, Johnston and Selander

1971, Gould and Johnston 1972, Zink and Remsen 1986). Geographic variation in quantitative phenotypic traits may arise through a number of processes including adaptation to the physical environ-

ment (McNab 1971, Geist 1987, Aldrich and James 1991, James 1991), coevolution in local communities (Brown and Wilson 1956), historical barriers to gene flow (Cracraft 1982, Patton et al. 1994), isolation by distance (Wright 1943, Aldrich and James 1991) and developmental plasticity and environmental induction (James 1983). Many processes are likely to influence species evolution, and nonheritable variation is likely to introduce uncertainty to adaptive interpretations of patterns.

Red-tailed Hawks (*Buteo jamaicensis*) are wide-ranging and show significant geographic variation in morphology (Schmidt 1994), plumage (Lish and Voelker 1986) and behavior (Knight et al. 1989). Preston and Beane (1993) listed 14 and recognized 13 North American subspecies (it is doubtful that *B. j. krideri* is a valid subspecies). These subspecies intergrade readily, but differences in plumage and morphometrics are apparent (Mindel 1983, Lish and Voelker 1986, Preston and Beane 1993). Such differences may be due to isolation in glacial refugia during the Pleistocene and, in the case of *B. j. harlani*, possible gene flow with *B. buteo* across Beringia (Mindel 1983). While we recognize that subspecific designations are imperfect, real phylogenetic entities can exist within species (McGillivray 1989, Avise 1994, Zink 1996). Such phylogenetic structure within species may need to be accounted for in evolutionary studies (Edwards and Kot 1995, Martins 1996). We focused on western North America, within the range of a single recognized subspecies, *B. jamaicensis calurus* (Fig. 1). Our analysis of geographic variation in Red-tailed Hawks was descriptive and exploratory. We examined the relationship between the physical environment and geographic variation within a large geographic area. We entertained several propositions in our discussion, but did not test any causal hypotheses.

METHODS

Specimens and Data. Museum skin specimens of *B. j. calurus* were designated "summer" or "winter" based on date of collection; specimens collected during the periods of peak migration given by Preston and Beane (1993) were excluded. Specimens were grouped into regions based on the second-order ecoregions of Bailey (Bailey 1976, Bailey et al. 1994, Ecological Stratification Working Group 1995) (Fig. 1). Specimens from the Sierra San Pedro Martir (SP) were treated as different from California Grasslands (CG) based on Dickerman (1994). Males and females were analyzed separately. Sex, location of collection, date of collection and subspecies, if designated, were recorded from the museum tag of each speci-

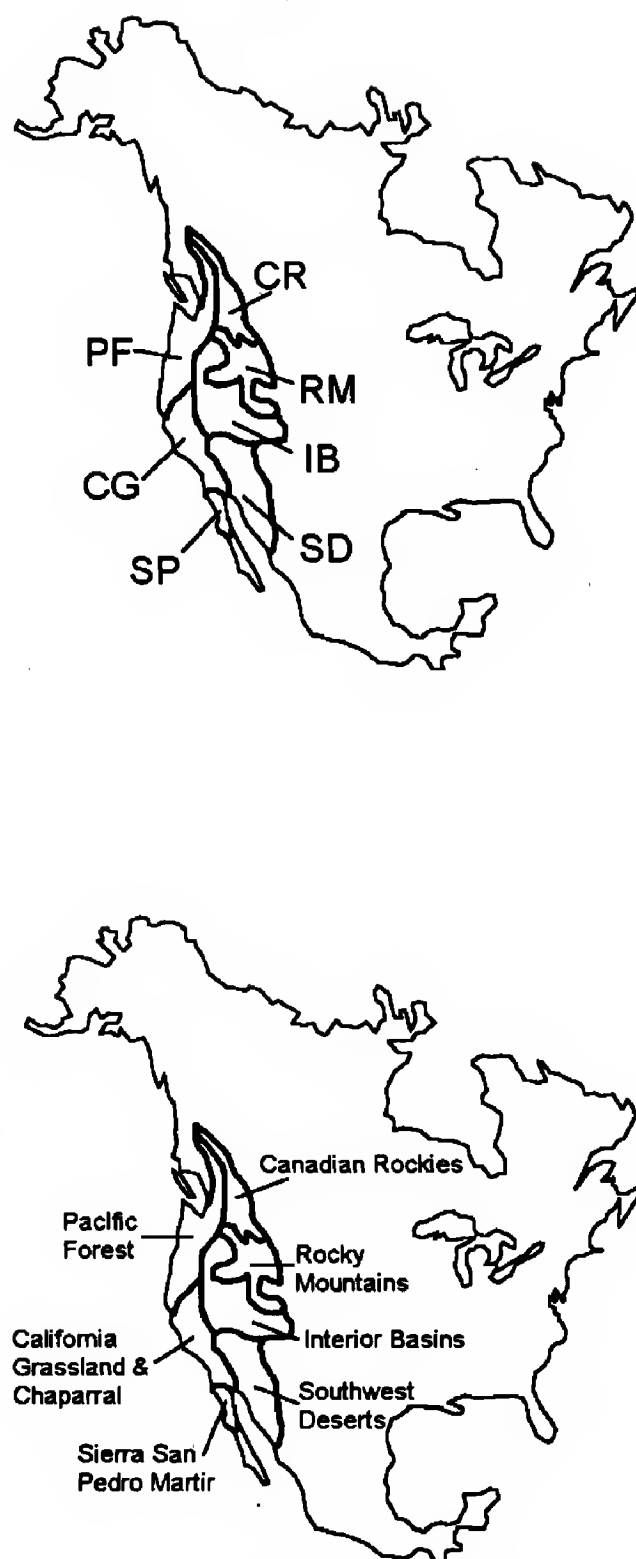


Figure 1. Regions: CG = California grasslands and chaparral, CR = Canadian Rockies, IB = Interior basins, PF = Pacific forests, RM = Rocky Mountains, SD = southwest deserts, SP = Sierra San Pedro Martir (Bailey 1976, Bailey et al. 1994).

men. Each collection location was matched up to the nearest weather station in the Meteorological Office (1980). Sample sizes are given in Table 1 and Fig. 2.

Six external measurements (in mm) were taken on each specimen. Measurements are described in the Golden Gate Raptor Observatory Bander's Training and Reference Manual (GGRO 1992), and were as follows: (1) wing chord (WC) = top of the wrist to the tip of the longest primary, (2) tail length (TA) = length of the longest middle retrix, (3) culmen (CU) = chord measurement of the exposed culmen, (4) tarsus depth (TD) = diameter of the narrowest section of the tarsometatarsus

Table 1. Likelihood ratio tests of independence and dimensionality of association between the set of morphological variables and the set of environmental variables. These were sequential tests of joint nullity of the smallest i through 4 canonical correlation coefficients, r_k^2 ($k = i, \dots, 4$). Bartlett's approximate χ^2 criterion was used according to Gittins (1985). $\chi^2 = -\{(N - 1) - \frac{1}{2}(p + q + 1)\} \ln \Lambda_i$. Wilks' $\Lambda = \prod_{j=1}^4 (1 - r_j^2)$.

i	ROOTS, r_k^2	r_i^2	df	WILKS'		P
				Λ	χ^2	
Summer males N = 41						
1	$r_1^2, r_2^2, r_3^2, r_4^2$	0.461	24	0.26	45.9	0.005
2	r_2^2, r_3^2, r_4^2	0.421	15	0.49	24.5	0.057
3	r_3^2, r_4^2	0.096	8	0.85	5.7	0.686
4	r_4^2	0.061	3	0.94	2.2	0.537
Winter males N = 55						
1	$r_1^2, r_2^2, r_3^2, r_4^2$	0.455	24	0.43	40.6	0.018
2	r_2^2, r_3^2, r_4^2	0.121	15	0.79	11.2	0.737
3	r_3^2, r_4^2	0.074	8	0.90	5.0	0.761
4	r_4^2	0.025	3	0.97	1.2	0.743
Summer females N = 43						
1	$r_1^2, r_2^2, r_3^2, r_4^2$	0.388	24	0.43	30.7	0.162
2	r_2^2, r_3^2, r_4^2	0.218	15	0.70	12.8	0.618
3	r_3^2, r_4^2	0.070	8	0.90	3.8	0.871
4	r_4^2	0.032	3	0.97	1.2	0.756
Winter females N = 49						
1	$r_1^2, r_2^2, r_3^2, r_4^2$	0.531	24	0.28	53.7	0.001
2	r_2^2, r_3^2, r_4^2	0.275	15	0.60	21.5	0.121
3	r_3^2, r_4^2	0.122	8	0.83	7.9	0.444
4	r_4^2	0.055	3	0.95	2.4	0.502

measured anteroposteriorly, (5) tarsus length (TL) = diagonal measurement from the medial bony protuberance of the ventral part of the proximal end of the tarsometatarsus to the joint of the middle digit and (6) hallux claw (HA) = chord measurement of the exposed hallux talon. The importance and reliability of tail length measurements are questionable due to feather wear.

Environmental variables obtained from the Meteorological Office (1980) were: Altitude (ALT), July maximum average daily temperature (JLMX), July minimum average daily temperature (JLMN), January maximum average daily temperature (JNMX), January minimum average daily temperature (JNMN) and annual precipitation (PPT).

Relative, rather than absolute, morphological measurements would have been desirable for certain comparisons. However, ratios present controversial statistical problems, especially in multivariate analysis (e.g., Albrecht 1978, Atchley and Anderson 1978, Pimintel 1979, but see James and McCulloch 1990). Further, without an independent measure of body size to work with, defining relative measures is problematic. WC has been used as an index of body size (e.g., Power 1969, James 1991).

Exploratory analysis of relative measures defined as ratios of our other measurements over WC or as residuals from simple linear regression on WC produced qualitatively similar results to those we present here (B. Fitzpatrick, unpubl. data).

Analysis of Regional Differences. Due to small sample sizes and potentially nonnormal data, we described differences among regions using box plots (McGill et al 1978, Benjamini 1988). A box plot displays a rectangle oriented on a coordinate system where the vertical axis has the scale of the data. The rectangle represents the middle half of the data, that is, its top and bottom are drawn at the upper and lower quartiles, respectively. The "whiskers" are drawn to the furthest value within 1.5 inter-quartile distances from the box. Data points outside of the whiskers are represented by thin horizontal lines and the median is represented by a thick horizontal line. With the data partitioned into regions, individual sample sizes were too small and uneven to make effective use of more formal statistical analyses (Fig. 2).

Analysis of Relationships Between Morphology and Climate. Multivariate relationships between morphology and physical environmental variables were investigated using canonical correlation (Gittins 1985, James and McCulloch 1990). Following Moran (1986), linear regression was used as a critical technique to assess confidence in patterns suggested by canonical correlation. This is an example of overlapping exploratory and critical data analysis (OCDA, Tukey 1982). Overlapping data analysis is a legitimate form of analysis, but it lacks the definitiveness of confirmatory analysis of carefully sampled independent data. In order to make more effective use of the linear techniques, ALT and PPT were log transformed as $x' = \log_{10}(x + 1)$ to adjust for skews to the right, and JNMN was transformed as $x' = (x + 21)^2$ to make all values positive and then adjust for a skew to the left (Zar 1984). Other variables showed approximately gaussian (normal) distributions. Analyses were performed using S-Plus 4.0 for Windows (MathSoft 1997).

Canonical correlation analysis. James and McCulloch (1990) reviewed statistical techniques in ecology and evolutionary biology. They argued that multiple regression analysis, a commonly used technique in this kind of study, has been overused and abused. They suggested that canonical correlation, although not free of limitations, may be more appropriate for descriptive ecomorphological studies. They stressed the descriptive role of multivariate analysis, and suggested deemphasizing formal statistical inference.

Our notation was that of Gittins (1985). Most simply, canonical analysis can be characterized as a generalization of multiple regression where there are multiple y variables in addition to multiple x variables. This analysis is appropriate when the attributes of a data set can be divided naturally into two sets (e.g., morphological and environmental measurements). If there are N observations, p x -variables, and q y -variables, canonical analysis generates two sample spaces, $\mathbf{Z}^{(x)}$ ($N \times p$) and $\mathbf{Z}^{(y)}$ ($N \times q$). Then, linear transformations of each set of variables, $u_i = \mathbf{a}_i' \mathbf{z}^{(x)}$ and $v_i = \mathbf{b}_i' \mathbf{z}^{(y)}$, are found simultaneously such that the simple correlation r_i between the canonical variates u_i and v_i is maximized. In all, s pairs of canonical variates are produced, $i = 1, \dots, s$ where s is the smaller

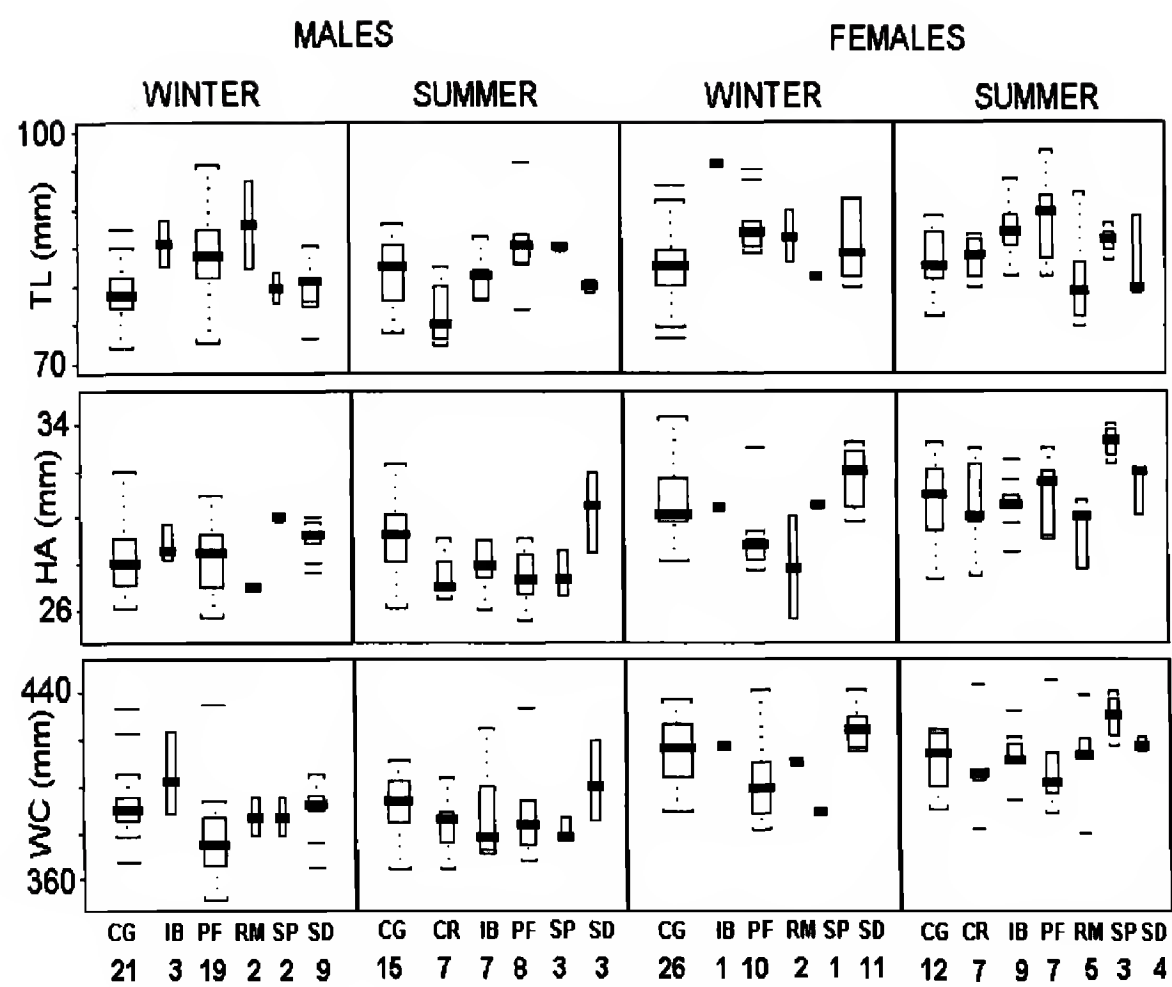


Figure 2. Box plots comparing some morphometric measurements of Red-tailed Hawks from different regions. Regions are identified in Fig. 1. Only those comparisons with marked differences are shown. The width of each box is proportional to sample size. Sample sizes are given along the bottom.

of p and q . Successive pairs of variates are required to be orthogonal to preceding pairs. Although multiple regression can be thought of as a special case where $q = 1$, it is important to note that in canonical analysis the two sets of variables are treated symmetrically. That is, it makes no difference which set is assigned to x and which is assigned to y ; both sets can be thought of as simultaneously predicting each other (Gittins 1985). Canonical correlation analysis is primarily a descriptive technique for exploring holistic relationships among variables of different kinds (Gittins 1985, Moran 1986, James and McCulloch 1990). Pimintel (1979), Gittins (1985), and Rencher (1995) are good references for canonical analysis.

RESULTS

Regional Differences. Only those box plots indicating differences among regions are shown in Fig. 2. Substantial variation among regions in TL, HA and WC was indicated for all groups, with summer females showing the weakest patterns and winter data sets the strongest (Fig. 2). WC and HA tended to be large in arid regions, while TL was generally greatest in the Pacific Northwest (PF).

Morphology and Environment. Squared canonical correlation coefficients, r_i^2 ($i = 1, 2, 3, 4$), are reported in Table 1. These coefficients express the

proportion of the variance of the i th morphological canonical variate that is accounted for by its conjugate environmental canonical variate (Gittins 1985). Values of r_1^2 ranged from 0.388–0.531 (Table 1), suggesting weak to moderate overall relationships between morphology and environment.

Independence. Likelihood ratio tests of the null hypothesis that the vector of morphological variables and vector of environmental variables were linearly independent are presented in the first line of each subtable of Table 1. Bartlett's χ^2 approximation lead to the rejection of linear independence for winter females and summer males ($P = 0.0005$ and 0.0046 , respectively). Evidence against independence for winter males was strong ($P = 0.0184$). The null hypothesis of independence for summer females should not be rejected by this analysis ($P = 0.1622$). These results suggested that Red-tailed Hawk morphology in western North America varies systematically with the physical environment.

Dimensionality. No significant relationship between morphology and environment remained after the first canonical correlation coefficients were eliminated (Table 1). Accordingly, we only exam-

Table 2. Correlations between original measurements and the first canonical variates. $JNMN^* = (JNMN + 21)^2$. $PPT^{**} = \log_{10}(PPT + 1)$.

MEASUREMENT	1ST CLIMATE	1ST MORPH
Summer males		
TL	0.19	0.28
TD	0.60	0.89
WC	0.24	0.35
TA	0.19	0.27
HA	0.49	0.73
CU	0.49	0.72
ALT	-0.23	-0.16
JLMX	-0.02	-0.01
JLMN	0.98	0.66
PPT**	-0.36	-0.25
Winter males		
TL	-0.51	-0.75
TD	0.11	0.16
WC	0.35	0.52
TA	0.27	0.40
HA	0.38	0.56
CU	-0.09	-0.14
ALT	0.16	0.11
JNMX	0.82	0.55
JNMN*	0.69	0.47
PPT**	-0.75	-0.51
Winter females		
TL	-0.46	-0.63
TD	0.42	0.58
WC	0.42	0.58
TA	0.20	0.28
HA	0.44	0.61
CU	0.41	0.56
ALT	-0.20	-0.15
JNMX	0.92	0.67
JNMN*	0.94	0.69
PPT**	-0.35	-0.25

ined the possible implications of the canonical variates corresponding to the largest root, r_1^2 (Gittins 1985). Summer females were not subjected to further analysis due to the independence of their morphological measurements to environmental variables in this small data set.

Canonical variates. We used the correlations between the original measurements and the first canonical variates to interpret the data (Table 2). Intraspecific correlations indicated that the first environmental variate primarily reflected temperature, although precipitation figured strongly in the winter males data set and only July *minimum* temperature

had a strong correlation in the summer males data set. The first morphological variate was moderately correlated with all variables except TA for winter females, strongly correlated with TL for winter males, and fairly strongly correlated with TD, HA and CU for summer males. Intra- and interspecific correlations were concordant (Table 2).

Linear regression. For winter males and females, the single temperature measure with the highest correlation with the first canonical variate was chosen for further analysis. The independent variables used for simple linear regression analyses were JNMN for winter females, JLMN for summer males, and JNMX and PPT for winter males. Regression analyses confirmed a negative relationship of TL with winter temperature ($P = 0.0005$ and $P = 0.0018$ for females and males, respectively), and positive associations with temperature for WC, TD, HA and CU (Table 3). A positive correlation between TL and PPT for winter males agreed with the observation of relatively long tarsi in the Pacific Forest region (Fig. 2). Results for males and females were concordant.

DISCUSSION

Wing chord, tarsus depth, tail length, hallux claw and culmen varied concordantly and were interpreted collectively to represent body size. Tail length clearly varied independently, its correlations with temperature and precipitation generally being opposite those of other measurements.

Bergmann's rule, which predicts that larger individuals are favored in colder environments because low surface area to volume ratios are advantageous in conserving heat, while smaller individuals dissipate heat more effectively in hot climates (Pianka 1988), is not supported by our results. In fact, size tended to be positively correlated with temperature. In large, well-insulated birds like Red-tailed Hawks, heat dissipation is probably accomplished mostly through the tarsi and feet (Mitgard 1980, Butler 1982, Gill 1990). Further, in cold areas, insulating feathers are likely to be more important than surface area in controlling heat loss, while the cost of heating a large body may be limiting (McNab 1971). Another thermoregulatory prediction, Allen's rule, states that individuals in hot climates should have longer appendages relative to body core size in order to dissipate heat more efficiently (Pianka 1988). It was also not supported by our data.

Positive correlation of winter male tail length with annual precipitation and positive correlations

Table 3. Simple linear regression analyses of morphological and environmental variables selected using canonical correlation. TL = tarsus length, TD = tarsus depth, WC = wing chord, HA = hallux length, CU = culmen length. JNMN = January minimum temperature, JNMX = January maximum temperature, JLMN = July minimum temperature, PPT = annual precipitation. $JNMN^* = (JNMN + 21)^2$, $PPT^{**} = \log_{10}(PPT + 1)$.

GROUP	DEPENDENT VARIABLE	INDEPENDENT VARIABLE	CORRELATION COEFFICIENT (r)	P-VALUE
Summer males	TD	JLMN	0.56	0.0001
	HA	JLMN	0.51	0.0006
	CU	JLMN	0.43	0.0048
Winter males	TL	JNMX	-0.41	0.0018
	TL	PPT**	0.38	0.0042
Winter females	TL	JNMN*	-0.48	0.0005
	TD	JNMN*	0.43	0.0019
	CU	JNMN*	0.38	0.0079
	WC	JNMN*	0.35	0.0136
	HA	JNMN*	0.35	0.0151

of the other variables, notably tarsus diameter with temperature, suggested that water stress rather than temperature could explain the clinal variation. Short, thick tarsi (smaller surface area to volume ratio) might reduce evaporative water loss. Despite the thermal disadvantage of large body size suggested by Bergmann's rule, larger individuals may be favored in arid regions by their ability to conserve water.

Climate may indirectly influence the development and adaptation of hawk morphology through variation in food types and availability. Overall size of animals may reflect food availability (Geist 1987, Zeweloff and Boyce 1988), while sizes of food capturing structures such as beaks and claws are likely to be adapted to the mode of foraging and the type of prey taken (Pianka 1988, Gill 1990). Prey type and availability both vary geographically. However, the large size of Red-tailed Hawks in southwest deserts and interior basins was inconsistent with a large effect of productivity on size. Rather, large size may be an adaptation to prey scarcity by increasing niche breadth (Reig 1992, Cohen et al. 1993).

Red-tailed Hawks vary in a systematic way within the range of *B. j. calurus*. They are largest in deserts and smallest in the wet Pacific Northwest, even in winter. This is generally the same as the pattern described for Northern Goshawks (*Accipiter gentilis*) (Squires and Reynolds 1997) and for 20 of 22 passerine species (James 1991). Further, tarsus lengths are relatively long in the Pacific Northwest in both Red-tailed Hawks and American Robins (*Turdus*

migratorius, Aldrich and James 1991). Morphometrics of widespread birds of disparate sizes and life histories exhibit concordant geographic variation, suggesting the need for a general explanation. James (1970, 1991) has proposed a "neo-Bergmannian" hypothesis, which emphasizes the interaction between moisture and temperature in their effects on thermoregulation; largest individuals are expected in cold and dry environments. Our results indicate that the role of temperature is less important for Red-tailed Hawks, and we suggest that water stress may modify and contribute to the neo-Bergmannian pattern.

Great Horned Owls (*Bubo virginianus*) are smallest in California, Baja California and the southwest, showing geographic size variation opposite to what we have described for Red-tailed Hawks (McGillivray 1989, Houston et al. 1998). Turkey Vultures (*Cathartes aura*) also appear to be smallest in California and the southwest, based on differences between subspecies described in Kirk and Mossman (1998). These conflicting trends testify to the complexity of causes of geographic variation. Even when the same selective pressures act on different populations, differences in their relative importance can cause different adaptive responses (McPeck 1996). Although sympatric species probably experience similar physiological challenges, different components of the physical environment (e.g., heat vs. water) may vary in importance among species. Further, selective pressures owing to diet, mating system, predation and competition are likely to interact in complex ways with the phys-

ical environment in creating the overall selective regime experienced by a population.

Although natural selection provides elegant hypotheses for the causes of morphological variation, this study was entirely descriptive; causal explanations await explicit tests. Statistically significant variations in body size and proportions may not be biologically significant in the functional morphology of Red-tailed Hawks (but see references in James 1991). The geographic variation described for Red-tailed Hawks is not necessarily adaptive or heritable. Morphometric differences that result from external factors during development may continue to vary regardless of gene flow and selection (James 1983). Further, environmental induction could explain concordant patterns among species as easily as selection. Analyses of the development, functional significance and quantitative genetics of morphometric variation are necessary to elucidate the implications of geographic patterns and environmental correlations.

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LITERATURE CITED

- ALBRECHT, G.H. 1978. Some comments on the use of ratios. *Syst. Zool.* 27:67–71.
- ALDRICH, J.W. AND F.C. JAMES. 1991. Ecogeographic variation in the American Robin (*Turdus migratorius*). *Auk* 108:230–249.
- ATCHLEY, W.R. AND D.R. ANDERSON. 1978. Ratios and the statistical analysis of biological data. *Syst. Zool.* 27:71–78.
- AVISE, J.C. 1994. Molecular markers, natural history, and evolution. Chapman & Hall, New York, NY U.S.A.
- BAILEY, R.G. 1976. Ecoregions of the United States (map). U.S. Forest Service, Ogden, UT U.S.A.
- , P.E. AVERS, T. KING AND W.H. McNAB. 1994. Ecoregions and subregions of the United States (Bailey's ecoregion map). (Prepared in cooperation with the ECOMAP Team of the Forest Service and the U.S. Geological Survey), USDA, For. Ser. <http://www.epa.gov/grd/bailey/>
- BENJAMINI, Y. 1988. Opening the box of a box plot. *Am. Stat.* 42:257–262.
- BROWN, W.L. AND E.O. WILSON. 1956. Character displacement. *Syst. Zool.* 7:49–64.
- BUTLER, R.W. 1982. Possible use of legs as dissipators of heat in flying Cliff Swallows. *Wilson Bull.* 94:87–89.
- COHEN, J.E., S.L. PIMM, P. YODZIS AND J. SALDANA. 1993. Body sizes of animal predators and animal prey in food webs. *J. Anim. Ecol.* 62:67–78.
- CRACRAFT, J. 1982. Geographic differentiation, cladistics, and vicariance biogeography: reconstructing the tempo and mode of evolution. *Am. Zool.* 22:411–424.
- DARWIN, C. 1859. On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. John Murray, London, U.K.
- DICKERMAN, R.W. 1994. Undescribed subspecies of Red-tailed Hawk from Baja California. *Southwest. Nat.* 39:375–378.
- ECOLOGICAL STRATIFICATION WORKING GROUP. 1995. A national ecological framework for Canada. Agriculture and Agri-Food Canada, Research Branch, Centre for Land and Biological Resources Research and Environment Canada, State of the Environment Directorate, Ecozone Analysis Branch, Ottawa/Hull. Report and national map at 1:7 500 000 scale. <http://199.212.18.77/~ecozones/>
- EDWARDS, S.V. AND M. KOT. 1995. Comparative methods at the species level: geographic variation in morphology and group size in Grey-crowned Babblers (*Pomastotomus temporalis*). *Evolution* 49:1134–1146.
- GEIST, V. 1987. Bergmann's rule is invalid. *Can. J. Zool.* 65:1035–1038.
- GGRO. 1992. Golden Gate Raptor Observatory bander's training and reference manual. 2nd Ed. Golden Gate Raptor Observatory, San Francisco, CA U.S.A.
- GILL, F.B. 1990. Ornithology. W.H. Freeman and Co., New York, NY U.S.A.
- GITTINS, R. 1985. Canonical analysis: a review with applications in ecology. Springer-Verlag, Berlin, Germany.
- GOULD, S.J. AND R.F. JOHNSTON. 1972. Geographic variation. *Annu. Rev. Ecol. Syst.* 3:457–498.
- HOUSTON, C.S., D.G. SMITH AND C. ROHNER. 1998. Great Horned Owl (*Bubo virginianus*). In A. Poole and F. Gill [EDS.], The birds of North America, No. 372. The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, DC U.S.A.
- JAMES, F.C. 1970. Geographic size variation in birds and its relation to climate. *Ecology* 51:365–390.
- . 1983. Environmental component of morphological differentiation in birds. *Science* 221:184–186.
- . 1991. Complementary descriptive and experimental studies of clinal variation in birds. *Am. Zool.* 31:694–706.
- AND C.E. McCULLOCH. 1990. Multivariate analysis in ecology and systematics: panacea or Pandora's box? *Annu. Rev. Ecol. Syst.* 21:129–166.
- JOHNSTON, R.F. AND R.K. SELANDER. 1971. Evolution in

- the House Sparrow. II. Adaptive differentiation in North American populations. *Evolution* 25:1–28.
- KIRK, D.A. AND M.J. MOSSMAN. 1998. Turkey Vulture (*Cathartes aura*). In A. Poole and F. Gill [EDS.], The birds of North America, No. 339. The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, DC U.S.A.
- KNIGHT, R.L., D.E. ANDERSON, M.J. BECHARD AND N.V. MARR. 1989. Geographic variation in nest-defense behavior of the Red-tailed Hawk *Buteo jamaicensis*. *Ibis* 131:22–26.
- LISH, J.W. AND W.G. VOELKER. 1986. Field identification of some Red-tailed Hawk subspecies. *Am. Birds* 40:197–202.
- MARTINS, E.P. 1996. Phylogenies, spatial autoregression, and the comparative method: a computer simulation test. *Evolution* 50:1750–1765.
- MATHSOFT. 1997. S-Plus User's Guide, S-Plus Programmer's Guide, S-Plus Guide to Statistics. Data Analysis Products Division, MathSoft, Seattle, WA U.S.A.
- MCGILL, R., J.W. TUKEY AND W.A. LARSON. 1978. Variations of box plots. *Am. Stat.* 32:12–16. [Also in The Collected Works of John W. Tukey, 1988, Volume V: Graphics, 1965–85. Wadsworth, Inc., Belmont, CA U.S.A.]
- MCGILLIVRAY, W.B. 1989. Geographic variation in size and reverse size dimorphism of the Great Horned Owl in North America. *Condor* 91:777–786.
- MENAB, B.K. 1971. On the ecological significance of Bergmann's rule. *Ecology* 52:845–854.
- MCPEEK, M.A. 1996. Linking local interactions to rates of speciation in communities. *Ecology* 77:1355–1366.
- METEOROLOGICAL OFFICE. 1980. Met. O. 856a. Tables of temperature, relative humidity, precipitation, and sunshine for the world. Part I: North America and Greenland (Including Hawaii and Bermuda). HMSO. London, U.K.
- MINDEL, D.P. 1983. Harlan's hawk (*Buteo jamaicensis harlani*): a valid subspecies. *Auk* 100:161–169.
- MITGARD, U. 1980. Heat loss from the feet of Mallards *Anas platyrhynchos* and arterio-venous heat exchange in the rete tibiotarsale. *Ibis* 122:354–358.
- MORAN, N.A. 1986. Morphological adaptation to host plants in Uroleucon (homoptera: aphididae). *Evolution* 40:1044–1050.
- PATTON, J.L., M.N.F. DA SILVA AND J.R. MALCOLM. 1994. Gene genealogy and differentiation among arboreal spiny rats (Rodentia: echimyidae) of the Amazon Basin: a test of the riverine barrier hypothesis. *Evolution* 48:1314–1323.
- PIANKA, E.R. 1988. Evolutionary ecology, 4th Ed. Harper Collins, New York, NY U.S.A.
- PIMINTEL, R.A. 1979. Morphometrics: the multivariate analysis of biological data. Kendall/Hunt. Dubuque, IA U.S.A.
- POWER, D.J. 1969. Evolutionary implications of wing and size variation in the Red-winged Blackbird in relation to geographic and climatic factors: a multiple regression analysis. *Syst. Zool.* 18:363–373.
- PRESTON, C.R. AND R.D. BEANE. 1993. Red-tailed Hawk (*Buteo jamaicensis*). In A. Poole and F. Gill [EDS.], The birds of North America, No. 52. The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, DC U.S.A.
- REIG, S. 1992. Geographic variation in pine marten (*Martes martes*) and beech marten (*M. fiona*) in Europe. *J. Mammal.* 73:744–769.
- RENCHE, A.C. 1995. Methods of multivariate analysis. John Wiley & Sons, Inc., New York, NY U.S.A.
- SCHMIDT, E.V. 1994. Morphological variation in migratory Red-tailed Hawks (*Buteo jamaicensis*) from the Goshute mountains of Nevada and the Manzano mountains of New Mexico. *J. Raptor Res.* 28:65.
- SQUIRES, J.R. AND R.T. REYNOLDS. 1997. Northern Goshawk (*Accipiter gentilis*). In A. Poole and F. Gill [EDS.], The birds of North America, No. 298. The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, DC U.S.A.
- TUKEY, J.W. 1982. Introduction to styles of data analysis techniques. Pages 1–11 in R. Launer and A.F. Siegel [EDS.], Proceedings of modern data analysis. Academic Press, New York, NY U.S.A. [Also in The Collected Works of John W. Tukey, 1986, Volume IV: Philosophy and Principles of Data Analysis, 1965–86. Wadsworth Advanced Books and Software, Monterey, CA U.S.A.]
- WALLACE, A.R. 1859. On the tendency of varieties to depart indefinitely from the original type. *Proc. Linn Soc.: Zool.* 3:59–62.
- WRIGHT, S. 1943. Isolation by distance. *Genetics* 28:114–138.
- ZAR, J.H. 1984. Biostatistical analysis, 2nd Ed. Prentice-Hall, Inc., Englewood Cliffs, NJ U.S.A.
- ZEVELOFF, S.I. AND M.S. BOYCE. 1988. Body size patterns in North American mammal faunas. Pages 123–148 in M.S. Boyce [ED.], Evolution of life histories of mammals, theory and pattern. Yale University Press, New Haven, CT U.S.A.
- ZINK, R.M. 1996. Comparative phylogeography in North American birds. *Evolution* 50:308–317.
- AND J.V. REMSEN, JR. 1986. Evolutionary process and patterns of geographic variation in birds. *Curr Ornithol.* 4:1–69.

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DIET OF THE MADAGASCAR HARRIER-HAWK, *POLYBOROIDES RADIATUS*, IN SOUTHEASTERN MADAGASCAR

SARAH M. KARPANTY¹

Department of Zoology, Miami University, Oxford, OH 45056 U.S.A.

STEVEN M. GOODMAN

Field Museum of Natural History, Roosevelt Road at Lake Shore Drive, Chicago, IL 60605 U.S.A.

ABSTRACT.—We recorded prey deliveries, pellets and food remains of the Madagascar Harrier-Hawk (*Polyboroides radiatus*) from 10 August–5 December 1997 at Berenty and Bealoka private reserves in extreme southeastern Madagascar. The Madagascar Harrier-Hawk had a variable diet, eating at least 16 prey species, including reptiles (2.4% of biomass), birds (11.5%), mammals (85.9%) and insects (0.2%). The largest component of the diet of the harrier-hawk in terms of biomass was Verreaux's Sifaka (*Propithecus verreauxi*), all of which were presented by the male to the female during courtship.

KEY WORDS: *Madagascar Harrier-Hawk*; *Polyboroides radiatus*; diet; lemur predation.

Dieta de *Polyboroides radiatus* en el sureste de Madagascar

RESUMEN.—Registramos las presas, egragópilas y restos de comida de *Polyboroides radiatus* desde Agosto 10 hasta Diciembre 5 de 1997 en las reservas privadas de Berenty y Bealoka en el extremo sureste de Madagascar. *Polyboroides radiatus* tuvo una dieta variable consumiendo por lo menos 16 especies distintas de presas, las cuales incluyen reptiles (2.4% de la biomasa), aves (11.5%), mamíferos (85.9%) e insectos (0.2%). El mayor componente de la dieta en términos de biomasa fue *Propithecus verreauxi*, todos aportados por el macho a la hembra durante el cortejo.

[Traducción de Autor]

Until recently, information on the diets of Malagasy raptors has been limited. Langrand (1990) summarized information based on stomach analyses of Rand (1936). More recent analyses of pellet remains of several owl species (Goodman and Thorstrom 1998, Goodman et al. 1993a, 1993b, Langrand and Goodman 1996) and the Madagascar Buzzard (*Buteo brachypterus*) (Goodman and Langrand 1996) have expanded our knowledge of this group. One endemic species of raptor for which little information is available is the Madagascar Harrier-Hawk (*Polyboroides radiatus*). Despite its abundance in a variety of habitats across the island ranging from montane rainforest to spiny desert scrub, little is known about the ecology of this raptor and there is no quantified information on its diet.

Recently, there has been an increased demand for information on the feeding ecology of Malagasy raptors. Conservationists concerned with protecting what remains of Madagascar's fragmented forests need to understand the ecosystem from the perspective of primary consumers. By focusing efforts on protecting predator populations such as raptors and the habitat containing their often large home ranges, we can more easily preserve organisms existing at all levels of the food chain (Watson and Lewis 1994). Primatologists have also become interested in documenting the diet of Malagasy raptors as they seek to understand the historic and present-day selection pressures on lemur life history characteristics. While predation on diurnal lemurs by the harrier-hawk has rarely been documented (Goodman et al. 1993), laboratory and field studies of lemur vigilance and alarm calls suggest that it may represent an important threat to free-ranging lemurs (Macedonia 1990, Sauther 1989). Wright (1998) demonstrated in a 10-yr be-

¹ Present address: Department of Ecology and Evolutionary Biology, SUNY at Stony Brook, Stony Brook, NY 11794-5245 U.S.A.

Table 1. Diet of the Madagascar Harrier-Hawk at Berenty and Bealoka Reserves in southeastern Madagascar. Data are combined from the two sites.

TAXA	MNI ^a	% TOTAL INDIVIDUALS	% TOTAL BIOMASS
Reptilia ^b			
<i>Furcifer lateralis</i>	1	1.6	0.1
<i>Tracheloptychus madagascariensis</i>	4	6.3	0.5
<i>Chalarodon madagascariensis</i>	1	1.6	0.1
<i>Dromicodryas quadrilineatus</i>	1	1.6	1.7
Aves ^c			
<i>Bubulcus ibis</i> (nestlings)	3	4.8	0.3
<i>Numida meleagris</i> ^d	1	1.6	4.3
<i>Streptopelia picturata</i>	1	1.6	0.8
<i>Coracopsis nigra</i>	3	4.8	2.8
<i>Coracopsis vasa</i>	2	3.2	2.4
<i>Acridotheres tristis</i> ^e	1	1.6	0.6
<i>Dicrurus forficatus</i> (nestlings)	4	6.3	0.3
Mammalia ^f			
<i>Propithecus verreauxi verreauxi</i> (adult)	2	3.2	29.1
<i>Propithecus verreauxi verreauxi</i> (young)	3	4.8	19.3
<i>Microcebus murinus</i> (adult)	3	4.8	0.6
<i>Microcebus murinus</i> (young)	1	1.6	0.1
<i>Tenrec ecaudatus</i>	4	6.3	33.4
<i>Rattus rattus</i> ^e (adult)	7	11.1	3.3
<i>Rattus rattus</i> (subadult)	1	1.6	0.2
Insecta (Orthoptera, Coleoptera, Lepidoptera)	20	31.7	0.2
Total	63	100	100

^a MNI = Minimum number of individuals.
^b Reptile biomass estimates provided by C. Raxworthy (pers. comm.).
^c Avian biomass from Goodman et al. (1997) and Telfair (1994).
^d Probably introduced to Madagascar (Langrand 1990).
^e Introduced to Madagascar.
^f Mammal biomass estimates from Mittermeier et al. (1994) and fieldwork by S.M. Goodman (pers. comm.).

havioral study that the large-bodied, diurnal rain-forest Milne-Edward’s Sifaka (*Propithecus diadema edwardsi*) responds to aerial predators such as the harrier-hawk by giving loud alarm calls, dropping low in the canopy and choosing daytime resting sites lower than feeding sites. The purpose of this study was to describe the diet of the Madagascar Harrier-Hawk.

STUDY AREA AND METHODS

Research was conducted between 10 August–5 December 1997 at the privately-owned Berenty and Bealoka Reserves in southeastern Madagascar (25°00’S; 46°18’E, elevation 100 m) near Amboasary-Sud, 80 km west of Tolagnaro (Fort Dauphin). Together, these two reserves compose approximately 200 ha of gallery and spiny forest on the banks of the Mandrare River and are dominated by *Tamarindus indica*, a characteristic tree of this semiarid thorn-scrub habitat. The climate of southern Madagascar

is characterized by a distinct dry season (March–November) and highly variable amounts of annual rainfall in the wet season (December–February). The forest fragments of Berenty and Bealoka are separated by 10 km of sisal plantations and small fragments of spiny forest; thus, there is no migration of primates between reserves. The land vertebrate faunal composition of the two reserves is essentially identical.

One occupied Madagascar Harrier-Hawk nest was found in each reserve in early August 1997 during the courtship stage of the breeding cycle. Birds were individually identified by key features. Species-specific vocalizations were used to assist in nest location. A blind was constructed adjacent to the nest tree within Berenty. Using 10 × 40 binoculars and a 30× spotting telescope, continuous observations of this nest were performed at half-day intervals in conjunction with lemur observations. Focal hours totaled 134 at this nest. Behavioral observations were not performed on the Bealoka nest.

Prey items brought to incubating or brooding parents were identified. Pellets and prey remains were also col-

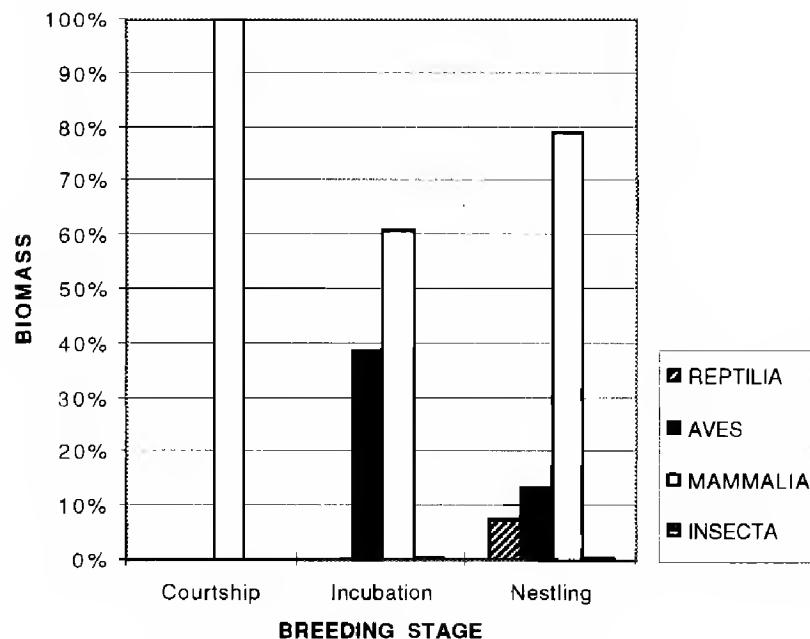


Figure 1. Percentage biomass of reptilian, avian, mammalian and insect prey of the Madagascar Harrier-Hawk during courtship, incubation and nestling stages of the breeding cycle based on direct observation of prey brought to the nest.

lected from beneath the nests. Prey collections at Berenty were made daily and at Bealoka weekly. Remains were sorted, dried and stored in plastic bags. Identification of prey remains was made to genus and species levels at the Université d'Antananarivo. Paired parts of any taxon were separated and the largest number of parts of either the left or right side was considered the minimum number of individuals (MNI). Data from the two nests were combined as data from the Bealoka nest were limited by the weekly collection schedule. The composition of the prey communities were identical between the two reserves.

RESULTS

Reptiles accounted for 11.1% of total individuals and 2.4% of total biomass, birds for 23.9% of individuals and 11.5% of biomass, mammals for 33.4% of individuals and 85.9% of biomass, and insects for 31.7% of individuals and 0.2% biomass of the diet during the nesting season (Table 1). The harrier-hawks had a generalist diet eating at least 16 different prey species, ranging from cockroaches (*Gromphadorhina portentosa*) to mouse lemurs (*Microcebus murinus*) and chameleons (*Furcifer lateralis*). One explanation for the relatively high diversity of prey types is the tendency for harrier-hawks to forage on the ground and probe tree holes and cavities as well as to hunt in flight and from perches.

Perhaps the most interesting result of our study is the heavy reliance of the harrier-hawks on mammalian prey. The harrier-hawks ate two adult (3.4 kg/individual) and three young (1.5 kg/individu-

al) Verreaux's Sifakas making this diurnal lemur the most important prey item for the hawks in terms of biomass (48.4%). All of the sifakas were taken during the courtship stage of the breeding season (Fig. 1). The large lipotyphlan tenrec (*Tenrec ecaudatus*), which weighs up to 1.95 kg, was the second most important prey item at 33.4% of total biomass. A small portion of the harrier-hawk's diet, either by numbers or biomass, consisted of introduced species (*Numida meleagris*, *Acridotheres tristis* and *Rattus rattus*).

DISCUSSION

Our study presents the first detailed analysis of the diet of the Madagascar Harrier-Hawk. Goodman and Pidgeon (1991) previously documented the consumption of a flying fox (*Pteropus rufus*) by harrier-hawks at Berenty and suggested that harrier-hawks may nest near and exploit concentrated food resources. Our study supports this finding. Not only did harrier-hawks eat sifakas, which are two to three times their body mass, but they also nested within 500 m of a heronry and consistently exploited this resource during the nestling stage of their breeding cycle. Rand (1936) reported remains of insects, spiders, lizards, frogs and small mammals in the digestive system of the Madagascar Harrier-Hawk. Our study demonstrates the diet of the harrier-hawk to be extremely variable, containing at least 16 vertebrate and invertebrate prey species. The continued success of this hawk in the fragmented forests of southern Madagascar will likely be due to its ability to exploit such a wide variety of prey.

One of the more striking findings of our study was the predation of harrier-hawks on large, diurnal lemurs. Evidently, harrier-hawks prey on both adult and infant Verreaux's sifakas and they can become seasonally the most important part of this raptor's diet in terms of biomass. Such predation might be detrimental for sifakas which typically produce one young per troop (7–8 individuals) per year. Our findings support the work of Rasoanindrainy (1985) who found that the main cause of sifaka mortality was predation by the Madagascar Harrier-Hawk. These findings should prompt primatologists to reconsider the importance of present-day predation pressure on lemur life-history characteristics (Csermely 1996). All predation by harrier-hawks on sifakas occurred during the courtship stage of the nesting cycle. Although data are limited, temporal variation in prey consumption

suggests that the sifaka may be difficult for this raptor to subdue, yet it is a valuable resource in the initial stages of nesting. Future research on the diet of the Madagascar Harrier-Hawk is needed to explore these seasonal differences in diet.

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LITERATURE CITED

- CSERMELY, D. 1996. Antipredator behavior in lemurs: evidence of an extinct eagle on Madagascar or something else? *Int. J. Primatol.* 17:349–354.
- GOODMAN, S.M. AND O. LANGRAND. 1996. Food remains found in a nest of the Madagascar Buzzard (*Buteo brachypterus*) in the Vohibasia Forest. Working Group on Birds in the Madagascar Region. 6:13–14.
- AND M. PIDGEON. 1991. Madagascar Harrier-Hawk *Polyboroides radiatus* preying on flying fox *Pteropus rufus*. *Ostrich* 62:215–216.
- AND R. THORSTROM. 1998. The diet of the Madagascar Red Owl (*Tyto soumagnei*) on the Masoala Peninsula, Madagascar. *Wilson Bull.* 110:411–415.
- , O. LANGRAND AND C.J. RAXWORTHY. 1993a. The food habits of the Barn Owl *Tyto alba* at three sites on Madagascar. *Ostrich* 64:160–171.
- , ——— AND ———. 1993b. Food habits of the Madagascar Long-Eared Owl, *Asio madagascariensis*, in two habitats in southern Madagascar. *Ostrich* 64:79–95.
- , S. O'CONNOR AND O. LANGRAND. 1993. A review of predation on lemurs: implications for the evolution of social behavior in small, nocturnal primates. Pages 51–66 in P.M. Kappeler and J.U. Ganzhorn [Eds.], *Lemur social systems and their ecological basis*. Plenum Press, New York, NY U.S.A.
- , M. PIDGEON, A.F.A. HAWKINS AND T.S. SCHULENBERG. 1997. The birds of southeastern Madagascar *Feldiana Zool.* 87:1–132.
- LANGRAND, O. 1990. Guide to the birds of Madagascar Yale Univ. Press, New Haven, CT U.S.A.
- AND S.M. GOODMAN. 1996. Note on the diet of the Madagascar Long-eared Owl (*Asio madagascariensis*) in the Special Reserve of Ambohitantely. Working Group on Birds in the Madagascar Region 6:9–11.
- MACEDONIA, J.M. 1990. What is communicated in the antipredator calls of lemurs: evidence from playback experiments with ring-tailed and ruffed lemurs. *Ethology* 86:177–190.
- MITTERMEIER, R.A., I. TATTERSALL, W.R. KONSTANT, D.M. MEYERS AND R.B. MAST. 1994. Lemurs of Madagascar. Conservation International, Washington, DC U.S.A.
- RAND, A.L. 1936. The distribution and habits of Madagascar birds. *Bull. Am. Mus. Nat. Hist.* 72:143–199.
- RASOANINDRAINY, J.M. 1985. Population dynamics of *Propithecus verreauxi*. *Nauchn. Dokl. Vyssh. Shk. Biol. Nauki* 4:43 (in Russian).
- SAUTHER, M.L. 1989. Antipredator behavior in troops of free-ranging *Lemur catta* at Beza Mahafaly Special Reserve, Madagascar. *Int. J. Primatol.* 10:595–606.
- TELFAIR, R.C., II. 1994. Cattle Egret in A. Poole and F. Gill [Eds.], *The birds of North America*, No. 113. The Philadelphia Academy of Natural Sciences, Philadelphia, PA and American Ornithologists' Union, Washington, DC U.S.A.
- WATSON, R.T. AND R. LEWIS. 1994. Raptor studies in Madagascar's rain forest. Pages 283–290 in B.-U. Meyburg and R.D. Chancellor [Eds.], *Raptor conservation today*. Pica Press, New York, NY U.S.A.
- WRIGHT, P.C. 1998. Impact of predation risk on the behavior of *Propithecus diadema edwardsi* in the rain forest of Madagascar. *Behaviour* 135:483–512.

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TWENTY YEAR CHANGE IN THE RAPTOR COMMUNITY IN NORTHERN UTAH DURING THE NONBREEDING SEASON

PHILLIP BROUSE

Fisheries and Wildlife, BNR 206, Utah State University, Logan, UT 84322-5210 U.S.A.

ABSTRACT.—Winter roadside surveys were conducted to count wintering raptors in Cache Valley, Utah. The study design allowed comparisons in distribution and species composition over the past 20 yr. Even though an increase in abundance was observed for American Kestrels (*Falco sparverius*), Merlins (*F. columbarius*), Bald Eagles (*Haliaeetus leucocephalus*) and Ferruginous Hawks (*Buteo regalis*), an overall decline was evident. Raptor numbers for the winter of 1997–98 were 61% of those reported for the winters of 1976–79. Despite changes in abundance and a change in geographic distribution, the temporal distribution remained the same. Raptor numbers were highest in irrigated pastures, followed closely by dry cropland. Numbers increased slightly from December–January, were lowest during February and rose steadily again through April.

KEY WORDS: *winter, raptor, roadside survey, Utah, abundance.*

Veinte años de cambio en la comunidad de rapaces del norte de Utah durante la estación sin reproducción

RESUMEN.—los Monitoreos de carretera fueron llevados a cabo para contabilizar rapaces durante el invierno en el Valle de Cache, Utah. El diseño del estudio permitió las comparaciones entre la distribución y la composición de especies en los últimos 20 años. Aunque se observó un aumento en la abundancia de *Falco sparverius*, *Falco columbarius*, *Haliaeetus leucocephalus* y *Buteo regalis*, un descenso se hizo evidente. Las cifras de rapaces para el invierno 1997–98 fueron 61% de aquellas reportadas por los inviernos de 1976–79. A pesar de los cambios en abundancia y los cambios en la distribución geográfica, la distribución temporal fue la misma. Los números de rapaces fueron mayores en pastizales irrigados seguidos de cerca por los cultivos en tierras secas. Las cifras se incrementaron levemente de Diciembre–Enero y fueron mas bajas en Febrero aumentando paulatinamente a través de Abril.

[Traducción de César Márquez]

Over the period of November 1976–March 1979, winter roadside counts were conducted to determine relative abundance, distribution and habitat use of raptors during the nonbreeding season in Cache Valley, Utah (Gessaman 1982). In the 20 yr since, both land use and the human population have changed. Winter raptor species composition and overall numbers have also changed. This study provides current data and a comparison of species composition and habitat changes that have occurred during the past two decades.

STUDY AREA

Cache Valley is located in northern Utah and southern Idaho. Its west boundaries are the Wellsville Mountains and the south and east boundaries are the Bear River Mountains. The northern border of the study area is the Utah-Idaho boundary. The average elevation is 1341 m and the land area surveyed was 68 088 ha.

METHODS

Where possible, the methods were consistent with those used by Gessaman (1982). The study area was divided into eight census areas which were surveyed once a month from December 1997–April 1998. Each census of all eight areas was completed within an 8-d period. Surveys were made by driving all accessible rural roads and randomly selected residential roads at speeds of less than 43 km/hr. Surveys were carried out in all types of weather where visibility was suitable. Each survey team consisted of a driver and up to three observers. At least one team member was proficient at raptor identification and the teams had field guides and binoculars on hand. Only raptors that were close enough to see with the unaided eye were counted.

Information recorded included species, habitat, sex, age, color morph or subspecies, map location, activity and perch type and height. The date, start and stop time, distance traveled, sky condition, air temperature, wind speed and snow depth were also noted for each survey. All sightings were also marked on a reusable laminated map of the area and transferred to overhead transparencies. Habitat was divided into the following types: ur-

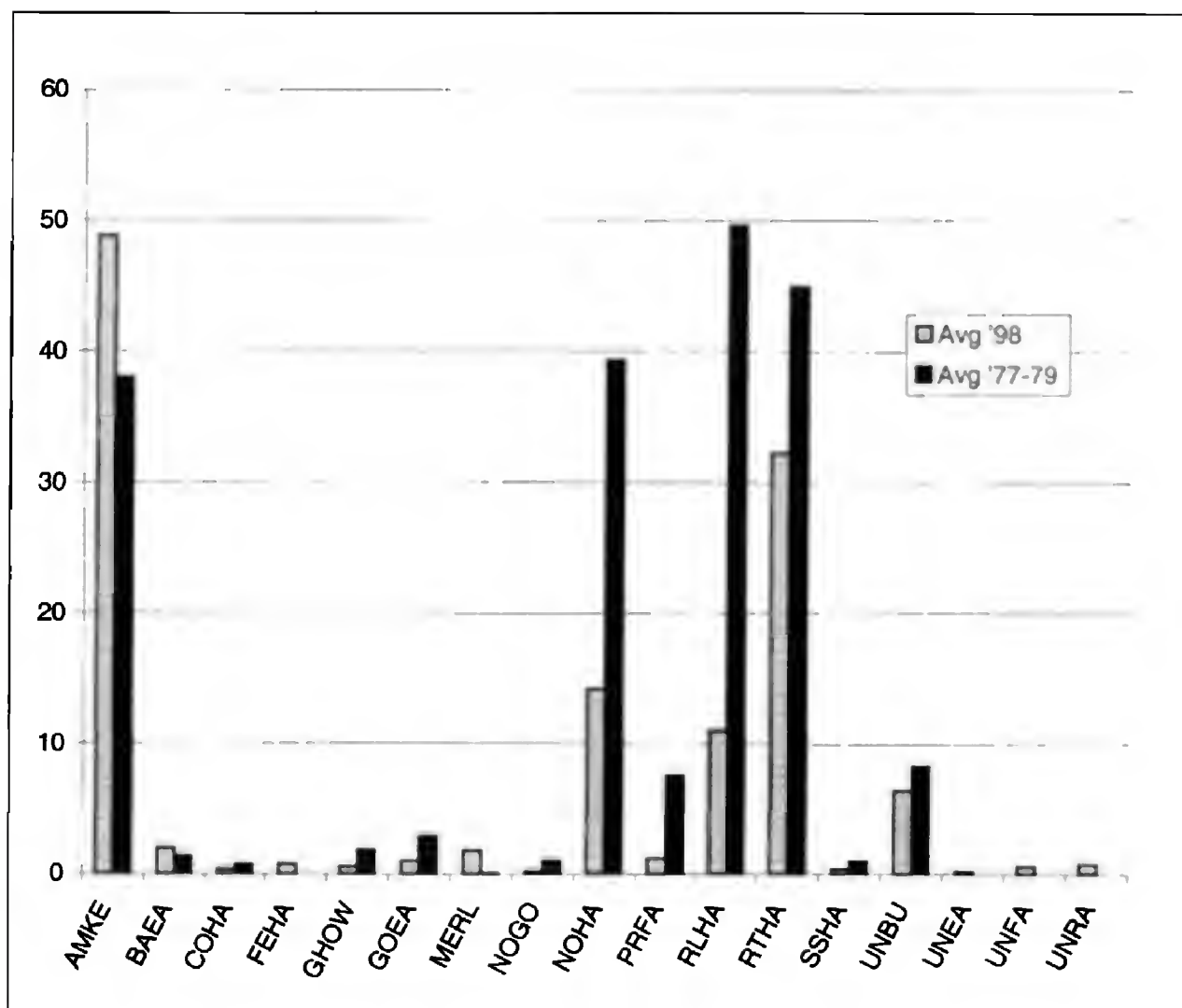


Figure 1. The average number of species of raptors observed in northern Utah in the nonbreeding season in 1977-79 and 1998.

ban, marsh, river floodplain, dry cropland, irrigated pasture/hay land, open water, native grassland and rural residential.

A relative abundance index was computed as described by Woffinden and Murphy (1977) as follows:

$$\frac{\text{Number of species observed}}{\text{Number of km traveled}} \times 1000$$

This is compatible with Gessaman (1982), who reported in units of observations per 1000 km.

RESULTS AND DISCUSSION

A total of 16 species was observed throughout the survey. Of these, three are summer residents and were observed only in April. Gessaman (1982) observed 18 species, one of which, the Harris's Hawk (*Parabuteo unicinctus*), was not native to Utah and probably escaped from a falconer. In all, 677 raptors were observed over the 4061 km driven. The overall relative abundance was 166.7, as compared to 272 reported by Gessaman. The average number of observations per survey was 135.4 (Fig. 1). Gessaman reported a considerably higher average of 221.25 per survey. Both the overall relative abundance and the average observations per sur-

vey for this study were 61% of Gessaman's observations. Both studies showed a similar temporal distribution with raptor numbers lowest in February (Fig. 2).

Mating behavior was noted as early as the second week in February for both American Kestrels (*Falco sparverius*) and Northern Harriers (*Circus cyaneus*). Red-tailed Hawks (*Buteo jamaicensis*) were not observed mating until April. Swainson's Hawks (*B. swainsoni*) had not yet returned during the mid-March survey, but were already nesting by the mid-April survey.

The winter of 1997-98 was an El Niño winter; however, the effects of El Niño on local migration patterns were not determined. It should be noted, however, that the winter of 1977-78 was also an El Niño winter.

For comparison, weather data were obtained from the Utah Climate Center at Utah State University for both study periods. The mean daily high temperatures for each month surveyed were similar for both studies with the exception of January (Fig. 3). The overall average number of days with

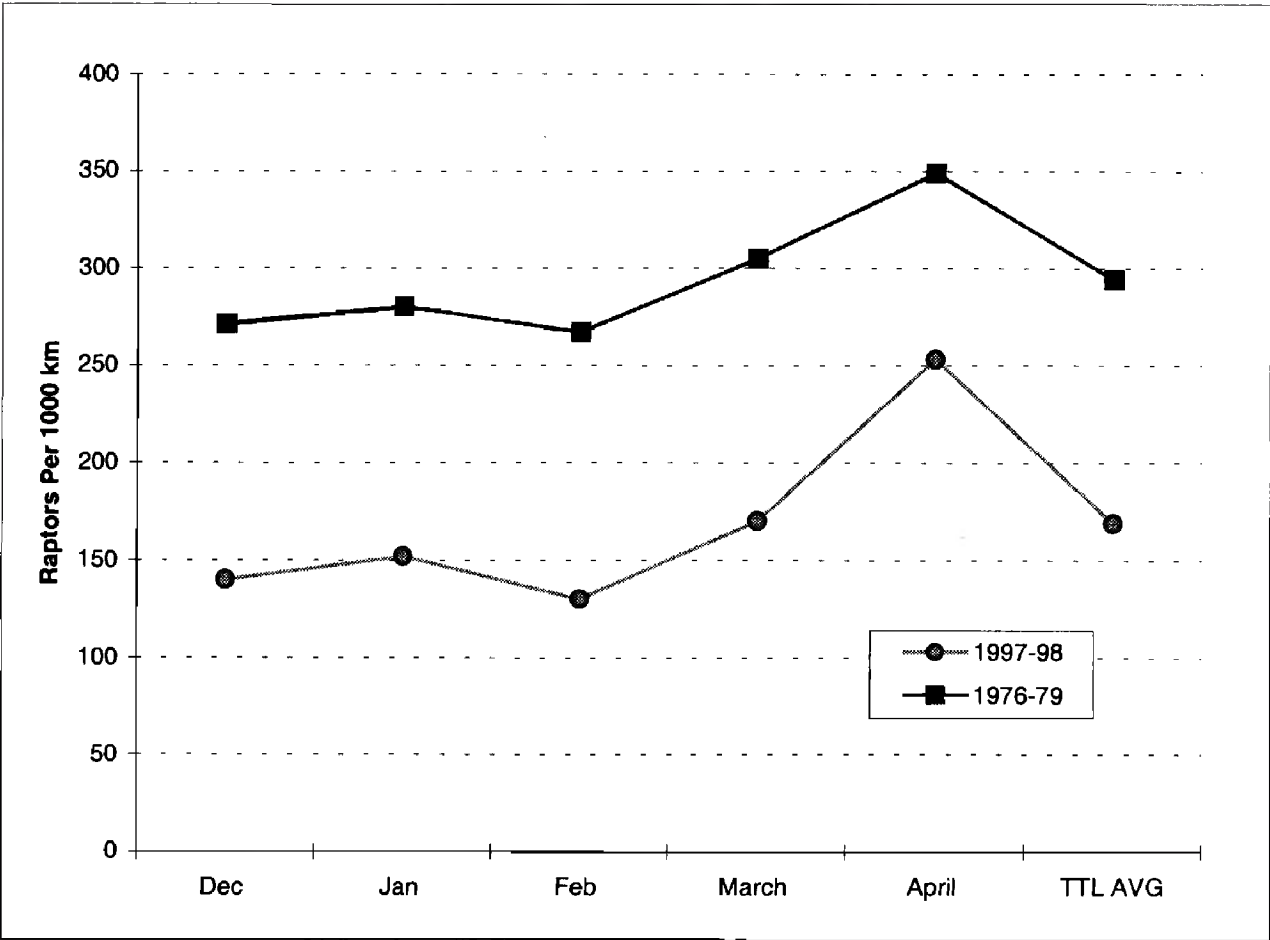


Figure 2. Monthly variation in raptor abundance in northern Utah during the nonbreeding season in 1976-79 and 1997-98.

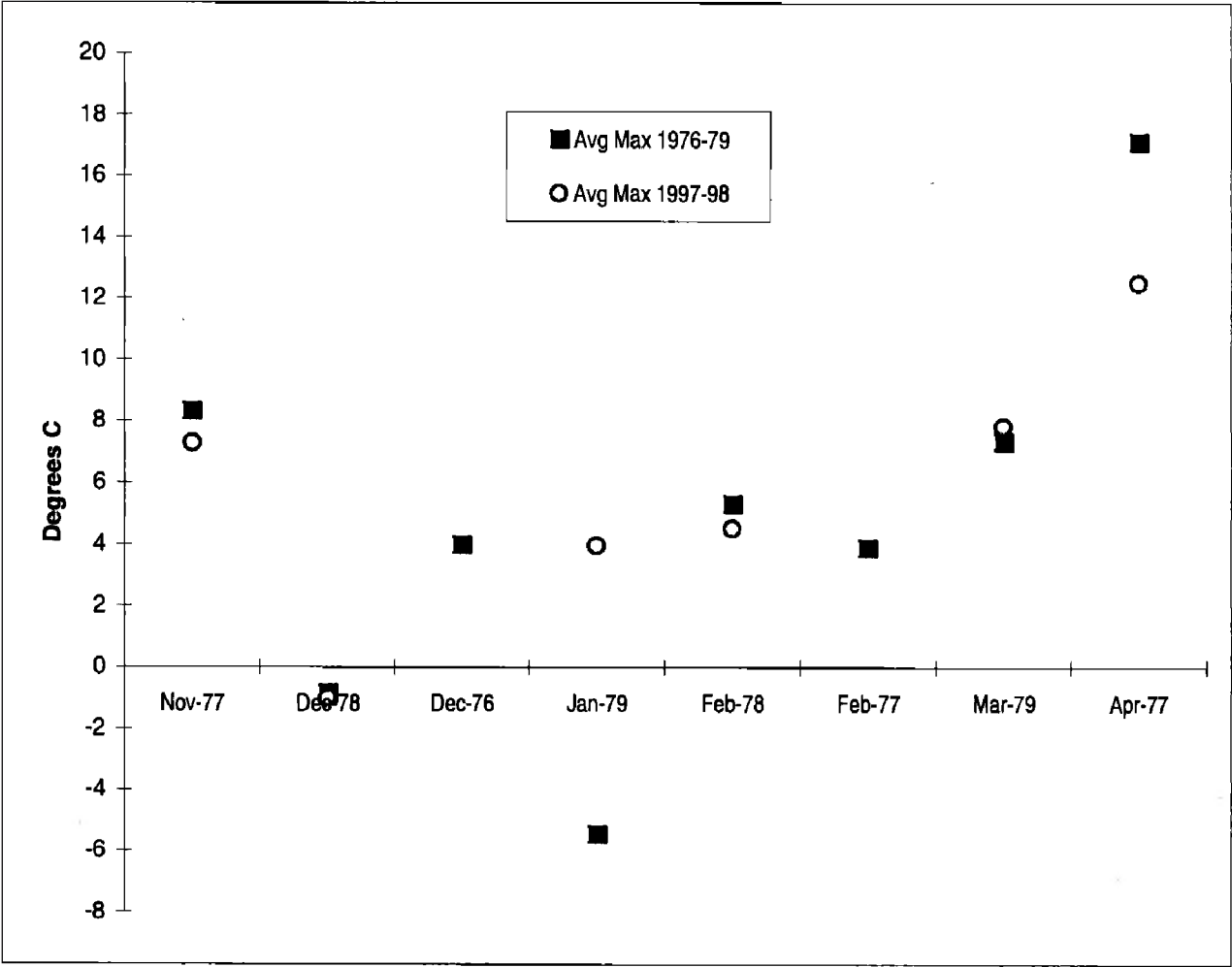


Figure 3. Mean daily high temperatures in northern Utah in 1976-79 and 1997-98.

Table 1. A comparison of observations of raptors in northern Utah in 1976–79 and 1998–99, excluding summer residents observed in April.

SPECIES	PER 1000 km		MEAN BIRDS PER CENSUS	
	1976–79	1998–99	1976–79	1998–99
American Kestrel	46.9	60.0	38.0	48.8
Bald Eagle	1.7	2.5	1.4	2.0
Cooper’s Hawk	1.0	0.5	0.8	0.4
Ferruginous Hawk	0.0	1.0	0.0	0.8
Great Horned Owl	2.3	0.7	1.9	0.6
Golden Eagle	3.6	1.2	2.9	1.0
Merlin	0.9	2.2	0.7	1.8
Northern Goshawk	1.2	0.3	1.0	0.2
Northern Harrier	48.5	17.5	39.3	14.2
Prairie Falcon	9.4	1.5	7.6	1.2
Rough-legged Hawk	62.1	13.5	49.6	11.0
Red-tailed Hawk	55.4	39.6	44.9	32.2
Sharp-shinned Hawk	1.2	0.5	1.0	0.4
Short-eared Owl	5.8	0.0	4.7	0.0
Unidentified buteo	21.9	7.9	17.7	6.4
Unidentified eagle	0.0	0.3	0.0	0.2
Unidentified falcon	0.0	0.7	0.0	0.6
Unidentified raptor	0.0	1.0	0.0	0.8
Totals	261.9	150.8	211.5	122.6

snow cover for the months surveyed by Gessaman was 12, while this study had an average of 14. The average number of days with snow cover per month was also similar, with the greatest difference (7 d) also being in January. Snow depth varied tremendously within the years surveyed by Gessaman. The winter of 1976–77 was close to average between the other two years and is similar to the winter of 1997–98. The 1976–79 averages ranged from 0.7–10.1 cm with a mean of 4.8 cm; the average snow depth for 1997–98 was 4.1 cm.

Most changes in habitat resulted from urban development on and below the benches along the eastern edge of the valley (areas three and eight). The development of industrial areas and the construction of apartments and low-income housing occurred within the valley on the western side of Logan (area six). In 1980, there was an estimated 18 864 housing units (U.S. Census Bureau 1996). This estimate increased to 27 595 units by 1997 (County-Wide Planning & Development Office 1998). The resident population increased from 52 423 in 1977 (U.S. Census Bureau 1996) to 87 907 in 1997 (County-Wide Planning & Development Office 1998). While total farmland decreased from 118 990 ha in 1978 to 108 427 ha in 1992, irrigated land remained similar (up from

35 256 ha to 35 401 ha), and dry cropland increased from 70 027 to 70 847 ha in the same period. The total amount of farmland in 1987 was 38.5% and in 1992 was 36% (U.S. Census Bureau 1996).

In Gessaman’s earlier study, the four most abundant species, Rough-legged Hawk (*B. lagopus*), Red-tailed Hawk, American Kestrel and Northern Harrier, had the highest densities in areas five, six and seven, although they were present in all census areas. While the same four species were the most abundant in this study (Table 1), they are distributed differently. Rough-legged Hawks were most abundant in areas one and six and absent from area three. Red-tailed Hawks were most abundant in areas four, six and seven, American Kestrels in areas two, six and seven, and Northern Harriers in areas one, five and six. Distribution for these species was not random over habitat types. Irrigated pasture was the most frequently used habitat, while dry cropland was the second most frequently used for all four species. The lack of Rough-legged Hawks in urban and suburban areas was consistent with the findings of Fischer et al. (1984) for central Utah.

Four species increased in relative abundance since Gessaman’s study. American Kestrels in-

creased from 46.9 to 60, Merlins (*F. columbarius*) from 0.9 to 2.2, Bald Eagles (*Haliaeetus leucocephalus*) from 1.7 to 2.5 and Ferruginous Hawks (*B. regalis*) from 0 to 1.0.

Among the buteos, the abundance of Rough-legged Hawks declined to 22% of the numbers reported by Gessaman. The 55 observations of this species accounted for 8% of all observations. Numbers were highest in January for both studies. Only one dark morph individual was seen, compared to 23 of 99 individuals observed by Gessaman.

A total of 161 Red-tailed Hawks was counted, accounting for 24% of all observations and constituting 72% of the numbers given for 1976–78. Gessaman reported that, of those identified to color, 22 were dark morphs and 116 were light morphs. During this study, 116 western light, six dark, nine rufous, three Harlen's and one Krider's morph Red-tailed Hawks were observed. One partial albino was also seen. The color was not recorded for 25 of the Red-tailed Hawks observed.

Seventy-one Northern Harriers were observed, with an average of 14.2 observations per census. Gessaman had an average of 39.3 Northern Harriers per census. Harriers were distributed more frequently over irrigated fields, then dry cropland, followed by marshland. However, marshland was usually nearby or interspersed with the other habitat type.

With a total of 244 observations, American Kestrels accounted for 36% of all observations and were the most numerous raptor. Of the observations where sex could be determined, 56% were male and 44% were female. My study found the greatest numbers in December with a steady decrease through March, for winter populations. Gessaman found the lowest numbers in December with a steady increase through March. The April numbers increased dramatically for both studies. My study saw numbers almost double from March–April, while Gessaman found that numbers more than quadrupled over the same two months. The kestrel was the only species to be frequently found in rural residential habitats, where it had its third highest frequency. The highest frequency was in irrigated pastures and the second was in dry cropland.

Nine Merlins were observed during the study, being absent only from areas one and three, both of which were on the edge of the valley. One Merlin was seen below a dam in an open riparian area with many snags, one in a rural residential area

and the others on pasture or cropland. Although *F. c. suckleyi* was not observed, both *F. c. richardsoni* and *columbarius* were. All three subspecies are known to winter in central Utah (Haney 1997).

Prairie Falcons (*F. mexicanus*) were observed at only 16% of the abundance reported in the earlier study. Six individuals were sighted, all of which were seen in December and January. Gessaman reported seeing them throughout the winter with the highest numbers in February.

Ten Bald Eagles, two of which were subadults, were observed. Six observations were known to be the same pair counted in three subsequent months. Bald Eagles were found near streams in open fields, even though Cache Valley's three reservoirs provided abundant open water and below-dam habitat. By comparison, Brown (1996) found that 88% of wintering Bald Eagles in Piedmont North and South Carolina were associated with below-dam habitats during the winter, instead of along rivers or near reservoirs. Five Golden Eagles (*Aquila chrysaetos*) were observed. Of these, four observations were known to be of the same pair.

One Northern Goshawk (*Accipiter gentilis*) was counted. Cooper's Hawks (*A. cooperii*) and Sharpshinned Hawks (*A. striatus*) both showed a decline, although accipiters were rare in both studies. Due to the survey design, areas with trees (urban and riparian habitats) were not surveyed as completely, thus all of the accipiters may not have been counted.

Short-eared Owls (*Asio flammeus*) were not observed during this study. Gessaman reported an abundance index of 5.8 with an average of 4.7 seen per survey. While casual observations indicated a local population crash in 1992, no data has been collected on this species for Cache Valley. This difference may have been due to chance encounters with groups of owls.

While the human population has risen and habitat has been lost, it is important not to assume a correlation between lower raptor numbers and increased human activity. The data may in part be the result of loss of habitat, but, as previously pointed out, most human growth has taken place in concentrated areas rather than in large portions of the study area. In most of the census areas, habitat remained as it was 20 years ago, leading me to believe that other factors, perhaps on the breeding grounds, have attributed to the decline.

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LITERATURE CITED

- BROWN, R.D. 1996. Attraction of Bald Eagles to habitats just below dams in Piedmont North and South Carolina. Pages 299–306 in [EDS.], *Raptors in human landscapes*. Academic Press, London, U.K.
- COUNTY-WIDE PLANNING & DEVELOPMENT OFFICE. 1998. Annual report of socio-economic characteristics, 1997 preliminary supplement. Logan, UT U.S.A.
- FISCHER, D.L., K.L. ELLIS AND R.J. MEESE. 1984. Winter habitat selection of diurnal raptors in central Utah. *Raptor Res.* 18:98–102.
- GESSAMAN, J.A. 1982. A survey of raptors in northern Utah, 1976–79. *Raptor Res.* 16:4–10.
- HANEY, D.L. 1997. Population dynamics of wintering Merlins (*Falco columbarius*) in central Utah. M.S. thesis, Brigham Young University, Provo, UT U.S.A.
- U.S. CENSUS BUREAU. 1996. U.S.A. counties 1996, Cache Valley, UT (49005), general profile. Washington, DC U.S.A.
- WOFFINDEN, N.D. AND J.R. MURPHY. 1977. A roadside census in the Eastern Great Basin—1973–1974. *Raptor Res.* 11:62–66.

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SHORT COMMUNICATIONS

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PRONOUNCED VARIATION IN TARSAL AND FOOT FEATHERING IN THE UPLAND BUZZARD (*BUTEO HEMILASIUS*) IN MONGOLIA

DAVID H. ELLIS

USGS Patuxent Wildlife Research Center, HCR 1 Box 4420, Oracle, AZ 85623 U.S.A.

NEIL WOFFINDEN

210 Engineering and Science Building, University of Pittsburgh at Johnstown, Johnstown, PA 15904 U.S.A.

PETER L. WHITLOCK

P.O. Box 325, Eastham, MA 02642 U.S.A.

P. TSENPEG

307 Sweet Avenue No. 7, Moscow, ID 83843 U.S.A.

KEY WORDS: *Upland Buzzard*; *Buteo hemilasius*; feather condition; *ptilosis*.

During 1994, 1995, 1997 and 1998, we located over 250 Upland Buzzard (*Buteo hemilasius*) nests across Mongolia. In these nests, we noted considerable morphological variation in plumage coloration and in leg pterylosis of nestlings. Although it is normal for many *Buteo* species to display a high degree of color polymorphism, the variability we found in tarsal and foot feathering was unique and sometimes greater within a single brood than could be expected within any naturally occurring raptor species.

Although Brown and Amadon (1968) illustrated the Upland Buzzard as bare-legged, their text states that the tarsus is partially feathered and Weick (1980) illustrated partial tarsal feathering. We found that more than half of the birds in Mongolia have fully feathered tarsi (Fig. 1a) while others, sometimes in the same nest, had tarsi three-quarters or even half feathered (Fig. 1b). Occasionally birds had patches of feathers or scattered feathers on their tarsi (Fig. 1b, c), and, less frequently, feathers on their toes (Fig. 1d).

Because of the variety of leg feathering that we observed during our first two expeditions, in 1997 and 1998 we examined 131 nests scattered across eastern and central Mongolia and report here the tarsal condition of 119 nestlings from 59 broods where young were at least 2 wk of age (i.e., we excluded younger nestlings to minimize confusion over ontogenic changes). Because developmental photos are unavailable for Upland Buzzards which Zhang (1984) claims fledge at 7 wk, we estimated

age by comparison with Moritsch's (1983) photos of Red-tailed Hawks (*B. jamaicensis*) which fledge at about 6 wk of age.

Feather condition was as follows: 69 nestlings had tarsi fully feathered (i.e., feathers extended [or would have extended when fully grown] from the ankle all the way to the base of the toes), 32 were three-quarters feathered and 18 were half feathered. Of the 119 nestlings, 16 had scattered feathers on their tarsi or feet beyond the zone of continuous feathering. Among the 69 nestlings with full tarsal feathering, four had scattered feathers between or on their toes. Another bird with only three-quarters feathered tarsi also had scattered feathers on its toes. Of the 11 nestlings with feathers scattered on their tarsi, eight were among the 18 nestlings with tarsi half feathered. For two nestlings, distribution of feathers was doubly odd. The lateral aspect of both tarsi were half feathered, while the medial sides were nearly fully feathered.

In summary, of 119 nestlings we carefully examined, 50 (42%) had less than fully feathered tarsi and four of the 69 with fully feathered tarsi had scattered feathers on their toes. Thus, 54 of 119 birds (45%) in some way deviated from the feathered tarsi-bare toes condition. Of this 54, 16 (13% of 119) had scattered feathers on either tarsi or toes. Observation of an occasional aberrant specimen in a population is not surprising, but for 13% of the population to exhibit such a conspicuous aberrancy (i.e., scattered feathers in otherwise scaled areas) strongly suggests allelic segregation beyond what would be expected without hybridization. Further, 42% of the young had significantly exposed (i.e., scaled) tarsi, even though



Figure 1a. Recently fledged, dark morph, Upland Buzzard from central Mongolia. This bird shows small pale breast patch suggestive of Long-legged Buzzard dark morph birds but fully feathered tarsus like about half of the Upland Buzzards in our sample. This bird is a brood mate of the fledgling in Fig. 1c. Figure 1b. Tarsi of Upland Buzzard nestlings in eastern Mongolia. Upper, half-feathered tarsus with a disjunct line or patch of feathers. Lower, three-

tarsal feathering has obvious adaptive advantages in cold climates.

The variability that we saw in tarsal feathering in the Upland Buzzard in Mongolia rivals the variability achieved after many generations of selective breeding in domestic varieties of chickens (*Gallus domesticus*) and Rock Doves (*Columba livia*). Poultry breeders have concluded that one or two independent autosomal genes are responsible for shank feathering in several breeds of chickens. The interaction of these genes produces the different patterns and the extent of feathering noted in various breeds (Hutt 1949). Three classes of leg feathering are recognized in pigeons, with the "grouse pattern" more closely resembling the condition observed in feather-legged raptors. The mechanism for inheritance of this trait is not clear, but the gene appears to be autosomal (Levi 1986). It is not uncommon in both poultry and pigeons for clean-legged birds to grow a few short feathers on the tarsi or show pin feathers on the toes. Levi (1986) found that a strain of clean-legged pigeons continued to throw some pin feathers after 35 yr of selection against feathered legs. Apparently more than one autosomal gene is responsible for these scattered feathers and the alleles responsible may be recessive.

The genetics of tarsal feathering in raptors is unknown, nor do we know of any publication indicating that there is any considerable variation for the trait within either feather-legged or bare-tarsi species. The extreme variation observed in Mongolian Upland Buzzards is believed to be unique. It is germane that some authors treat the Upland Buzzard as conspecific with the Long-legged Buzzard (*B. rufinus*, Vaurie 1961), a species with bare tarsi (Brown and Amadon 1968, Weick 1980). It is pertinent that the only bare-legged Upland Buzzard we noted on any of our expeditions was in western Mongolia and within Vaurie's (1961) zone of Upland and Long-legged Buzzard sympatry. Also pertinent to the hybridization question is Vaurie's (1961) map showing that the easternmost extension of the breeding range of the Upland Buzzard is only 600 km west of and at the same latitude as the southern extension of the range of the Rough-legged Buzzard (*B. lagopus*), a species with consistently feathered tarsi. Galushin (1981) mentions a nesting record of the Upland Buzzard on the Amur River that is even further east than the eastern limit mapped by Vaurie. Further, Vaurie shows that Rough-legged Buzzards occasionally breed only about 700 km north of the western range of both Upland and Long-legged Buzzards. There is re-

markable similarity between many light morph Rough-legged and Upland Buzzards. Further, many dark morph Upland and Long-legged Buzzards have a unique light crescent on an otherwise dark breast and both sometimes have a light patch on the crown and forehead (Brown and Amadon 1968, Plate 107; Fig. 1a, c).

The most likely explanation of this tarsal and foot feathering anomaly and these plumage similarities is that extensive hybridization is ongoing between Upland and Long-legged Buzzards. Alternately, the Upland Buzzard may be the result of a major hybridization event between Long-legged and Rough-legged Buzzards in the recent past. If either (or both) of these possibilities is (are) true, we expect that careful morphological comparisons for other anatomical features of Upland Buzzard specimens will also show extreme variability. Another, but we think unlikely, explanation is that the variability that we noted is simply the norm for the Upland Buzzard.

In explaining this anomaly, it may be helpful to examine Rough-legged Buzzard nestlings around the Sea of Okhotsk and Long-legged Buzzard nestlings in northwestern China and eastern Kazakhstan, or other zones of sympatry with the Upland Buzzard. Field teams working outside of Mongolia could provide useful comparative data on other Upland Buzzard populations as well. In 1997, we gathered blood samples for genetic analysis in the expectation that comparison of DNA for the three "species" will ultimately resolve this interesting question.

RESUMEN.—Casi la mitad de 119 pichones de *Buteo hemilasius* observados en Mongolia, mostraron tarsos y garras emplumadas en forma distinta a lo esperado (tarsos emplumados, garras desnudas). Muchos mostraron parches de plumas en áreas desnudas de tarsos y garras. Este extraordinario grado de variabilidad puede ser explicado como el resultado de una extensiva y reciente hibridación entre *Buteo rufinus* y *Buteo lagopus* y/o entre *Buteo rufinus* y *Buteo hemilasius*.

[Traducción de César Márquez]

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fourths feathered tarsus. Figure 1c. Fledgling, dark morph Upland Buzzard (brood mate of the bird in Fig. 1a) with extensive pale patches on breast and head like that known for the dark morph of the Long-legged Buzzard. The tarsus is half feathered with a more distal, disjunct patch of feathers. Figure 1d. Tarsi of nestling Upland Buzzards in eastern Mongolia. Both birds will have fully feathered tarsi (when hard-penned) and both have a scattering of feathers on the toes.

LITERATURE CITED

- BROWN, L. AND D. AMADON. 1968. Eagles, hawks and falcons of the world. Vol. 2. McGraw-Hill, New York, NY U.S.A.
- GALUSHIN, V.M. 1981. Changes in population status and nest range distribution of Falconiforms in the USSR since 1950. *Raptor Res.* 15:4–11.
- HUTT, F.B. 1949. Genetics of the fowl. McGraw-Hill, New York, NY U.S.A.
- LEVI, W.M. 1986. The pigeon. Levi Publishing Co., Inc., Sumpter, SC U.S.A.
- MORITSCH, M.Q. 1983. Photographic guide for aging nestling Red-tailed Hawks. USDI/BLM Snake River Birds of Prey Project, Boise, ID U.S.A.
- VAURIE, C. 1961. Systematic notes on Palearctic birds. No 47. Accipitridae: the genus *Buteo*. *Am. Mus. Novit.* 2042:1–13.
- WEICK, F. 1980. Birds of prey of the world. Verlag Paul Parey, Hamburg and Berlin, Germany.
- ZHANG, X. 1984. Measurements of growth, development and daily energy intake of Upland Buzzard nestlings. [In Chinese with English summary.] *Zool. Res.* 5:369–376.

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CLOSE INBREEDING IN PEREGRINE FALCONS IN MIDWESTERN UNITED STATES

HARRISON B. TORDOFF

Bell Museum of Natural History and Dept. of Ecology, Evolution and Behavior, 1987 Upper Buford Circle, University of Minnesota, St. Paul MN 55108 U.S.A

PATRICK T. REDIG

The Raptor Center, 1920 Fitch Ave., University of Minnesota, St. Paul MN 55108 U.S.A.

KEY WORDS: *Peregrine Falcon*; *Falco peregrinus*; *close inbreeding*; *midwestern United States*

Selection against inbreeding is usually assumed to be an important factor in the evolution of dispersal patterns in animals (Thornhill 1993), because close inbreeding increases the probability of expression of deleterious recessive genes. We have identified several cases of close inbreeding (here defined as mating between siblings, half-siblings or parents and offspring) in Peregrine Falcons (*Falco peregrinus*) in the midwestern United States. This paper discusses the possible causes and consequences of these inbreeding events.

The current midwestern peregrine population originated from 857 captive-bred falcons released since 1982 as a part of the continent-wide effort to reestablish populations of the species in areas where they had been eliminated or reduced by poisoning by DDT and related compounds. Midwest as here used includes Minnesota, Wisconsin, Michigan, Nebraska, Iowa, Illinois, Indiana, Ohio, Kansas, Missouri, Kentucky, southeastern Manitoba and the Lake Superior basin of Ontario. We have already shown for this new population (Tordoff and Redig 1997), numbering 99 territorial pairs in 1998, that: 72% nest on man-made structures and 28% on cliffs. First breeding is usually at age two, although some females and fewer

males begin at one year of age. First-year survival is probably close to 40% and annual survival of adults is 86%. Dispersal from hatch or natal sites has huge variation (range 0–>1500 km for both sexes, but mean dispersal of females (323 km) is about twice that of males (176 km).

Peregrines released in the restoration effort have passed through three bottlenecks, each of which must have reduced genetic variation in the population. The first was the pesticide-induced reduction in size of wild populations from which captive birds were drawn. Second, captive-breeding peregrines represented a small sample of the wild populations from which they were taken. The number of true founders (unrelated ancestors brought in from the wild for captive breeding) for the new midwestern population was 70–80 individuals. Third, a founder's contribution of genetic material to the wild population is determined by differential reproduction in captivity, which is probably more pronounced than in the wild.

Only about one-fourth of fledged young, released or wild-produced, actually become breeders in the wild. Through 1996, 1383 peregrines were known to have fledged in the Midwest (757 hatched, 626 wild); through 1998, about 290 (21%) of these were known to have become breeders, although some additional birds fledged

Table 1. Close inbreeding in nesting (eggs laid) midwestern Peregrine Falcons.

FEMALE	MALE	RELATIONSHIP AND PLACE OF FLEDGING	NESTING LOCALITY
Mae 31T	13T	Half-siblings from different wild broods, same mother, different fathers; Minneapolis MN	NSP King, Bayport MN
Mae 31T	Jim 51Z	Mother, son, both wild fledged; Minneapolis and Bayport MN	NSP King, Bayport MN
Mae 31T	Caesar 49Z	Full siblings from different wild broods; Minneapolis MN	NSP King, Bayport MN
Skywalker U/R	55X	Half-siblings from different wild broods, same mother, different fathers; St. Paul MN	NSP Black Dog, Eagan MN
Sunrise 55R	Cinder 5/C*	Mother, hacked Cincinnati OH, 1-yr old son, wild Detroit MI	Whittier Apartments, Detroit MI
Carmen D/N	C/U	Full siblings from different wild broods, Milwaukee WI	Commodore Perry, Toledo OH
Suzy Q 52P	Doc 55Y	Full siblings, same age, hacked together at Grand Rapids MI	U.S. Steel, Gary IN

* Two captive-produced young added to nest fledged.

in 1996 or earlier will still enter the breeding population in future years. Given first-year survival of 40% and annual survival of territorial adults of 86%, one would expect 34% of fledged peregrines to survive to the end of their second year, 30% to the end of the third year. The discrepancy between the observed 21% that became breeders and the predicted 30% that survived to age three showed that living to adulthood was not a guarantee of becoming a breeder. It is still necessary to find a territory and a mate. Further, the 86% annual survival of territorial adults probably overestimates survival of non-territorial adults, which have to cope daily with unfamiliar surroundings (Ratcliffe 1980).

We identified 17 nestings (4% of a total of 454 from 1987–98) by seven pairs of peregrines in the Midwest in which the adults (5 females, 7 males) were related as half-siblings, full siblings or mother and son (Table 1). What behaviors in peregrines act to minimize inbreeding? Two obvious possibilities are dispersal tendencies and avoidance of potential mates known from memory to be close relatives. Peregrines are highly mobile and capable of long distance dispersal. Since dispersal directions of individuals fledging from the same site are generally random, the dispersal distances typical of midwestern peregrines should minimize incestuous pairings. Further, females disperse on average about twice as far as males, increasing the odds against sibling matings. The short dispersal distances of some individual midwestern peregrines early in the restoration program reflected the lack of competition for suitable breeding sites in a growing population. As the peregrine population approaches carrying capacity and suitable territories become more difficult to find, the opportunity for short distance dispersal between natal and subsequent breeding site should diminish.

Can peregrines recognize same-age siblings, offspring

and previous mates? Is their memory good enough to permit recognition of these relatives from one year to another? Might peregrines recognize in some way close relatives that they have not previously encountered, such as older or younger siblings? These questions cannot be answered convincingly with the evidence available, but some comments seem justifiable. The long-term memory of peregrines, like that of other migratory birds, is clearly adequate for performing impressive feats of migration. Many western hemisphere peregrines move over half the globe, from Alaska and Greenland to southern South America. Recognition of landmarks, however, does not necessarily guarantee recognition of individuals. Territorial peregrines obviously recognize their current mates visually (and probably vocally) and respond to intrusions of strange peregrines at substantial distances. Further, it is clear that peregrines can easily recognize the sex of other peregrines, much more efficiently than can experienced human observers. On territory, females usually chase out intruding females and males likewise usually chase males. Territorial adults appear to recognize intruders as such, but usually refrain from aggressive challenges of intruders of the opposite sex. Unpaired adults on territory seem willing to accept any adult of the opposite sex. No conclusive evidence exists either way that pairs from the previous year, separated over winter, recognize each other at reunion. In at least a dozen cases in the Midwest, we have identified occupants of territories in early spring to comprise one bird from the previous year and a new individual. Usually, the other bird from the previous year has returned and evicted the new bird. If the first bird from the previous year favored either of the struggling birds, it was not obvious.

Parental peregrines in captivity and in the wild accept their own young and augmented young without prejudice, even up to the early days after fledging. Even young

of inappropriate age are usually accepted, such as 10-d-old young given to adults in place of a clutch of only partially incubated eggs. Young in a brood, whether wild birds or young being hacked, seem to discriminate among members of their group, acting aggressively toward some individuals, friendly toward others and submissive to some. Despite the subjectivity of these observations, it seems fair to conclude that peregrines of all ages have the ability to recognize and discriminate among other individuals over the short term, although parental behavior may override such recognition in favor of guaranteed care of all young in a nest. Selection to identify own nest contents by breeders would not exist because mixing does not occur in nature. Whether short-term ability to recognize other individuals carries over from year to year and might be useful in avoiding close relatives as mates is less obvious.

Pairings of full siblings or half-siblings from different broods (Bayport, Eagan and Toledo pairs, Table 1) without prior contact seem to be matters of mere chance. Avoidance of pairings between siblings from the same brood would require individual recognition persisting over a year or more. There is no evidence that peregrine siblings remain together through the winter. Similarly, avoidance of parent-offspring pairings (Bayport) would require long-term memory of individuals (assuming separation over winter), which, if present in peregrines, is clearly not wholly effective in eliminating such incestuous relationships. In Detroit, Sunrise 55R paired in 1997 with an unbanded male and fledged one young, a male that remained with her on the nesting territory through the winter, mated with her in 1998, and fledged two young (J. Yerkey, unpubl. data), suggesting that even recognition of the parent-offspring relationship by both birds was not a deterrence to mating. Finally, siblings released at hack sites (Gary pair) experienced enough disrupted interactions with their own parents and enforced interactions with nonrelatives before release to make futile any effort to understand the effect of long-term memory on their later pairing propensities. So far, we have seen no instances of full sibling wild brood mates pairing in later years, but this may be simply a matter of small sample size.

These instances of inbreeding suggest that avoidance of incest by recognition of close relatives is ineffective and that dispersal behavior is the primary, perhaps exclusive, mechanism for avoidance of close inbreeding in Peregrine Falcons.

In none of the close-inbreeding pairings described here was there any obvious indication of genetic problems in the offspring which might have been expressed through exposure of deleterious recessive alleles. All 37

young appeared to be normal and breeding success did not differ from the rest of the population (2.2 young per nesting for the inbreeding pairs, 2.1 young per nesting for the whole population). The fact that the new population has passed through three bottlenecks ensures loss of some genetic variability, including deleterious alleles as well as normal ones. Further, like all organisms, peregrines are routinely subject to rigorous selection against alleles that might impair their fitness. Although the global population of peregrines is large, they occur mostly at low density, lowering the effective population size despite their mobility. This would favor, by fostering inbreeding, the expression of and consequent selection against deleterious recessive alleles. All these factors may have functioned to minimize levels of deleterious alleles in peregrine populations, which would result in less rigorous selection against close inbreeding.

RESUMEN.—En el oeste medio de los Estados Unidos, 17 eventos de entrecruzamientos cercanos (copulas entre hermanos, medio-hermanos y padres e hijos) de halcones peregrinos (*Falco peregrinus*) han sido documentados. El evitar el entrecruzamiento en esta especie parece ser el resultado del comportamiento de dispersión (a la suerte en dirección, la media de la distancia de dispersión de las hembras es el doble de la de los machos) mas que la memoria a largo plazo y el reconocimiento de parientes cercanos.

[Traducción de César Márquez]

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LITERATURE CITED

- RATCLIFFE, D. 1980. The Peregrine Falcon. Buteo Books, Vermillion, SD U.S.A.
 THORNHILL, N.W. [ED.]. 1993. The natural history of inbreeding and outbreeding. Univ. Chicago Press, Chicago, IL U.S.A.
 TORDOFF, H.B. AND P.T. REDIG. 1997. Demography of midwestern Peregrine Falcons, 1982–1995. *J. Raptor Res.* 31:339–346.

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DISTRIBUTION AND HABITAT USE OF SHARP-SHINNED AND COOPER'S HAWKS IN ARKANSAS

HEATH D. GARNER¹

Southern Ecological Services, 1204 Arrowhead Farm Road, Jonesboro, AR 72401 U.S.A.

KEY WORDS: *Cooper's Hawk*; *Accipiter cooperii*; *Sharp-shinned Hawk*; *Accipiter striatus*; *nest sites*; *pine plantations*; *nesting success*.

Cooper's (*Accipiter cooperii*) and Sharp-shinned (*A. striatus*) Hawks are considered uncommon to rare residents of Arkansas by the Arkansas Game and Fish Commission (K. Rowe pers. comm.). Only casual observations on nesting attempts by the two species have been reported in Arkansas (James and Neal 1986), and no recently-confirmed nesting attempts have been reported (K. Rowe, T. Foti pers. comm.). This lack of nesting data has been due to the inability of Breeding Bird Surveys or other contemporary bird monitoring techniques to detect nesting accipiters (Rosenfield and Bielefeldt 1993). This study was undertaken to conduct a survey of nesting Sharp-shinned and Cooper's Hawks and to describe the nesting habitats used by these species in Arkansas.

METHODS

Nest locations were found by using three methods. First, posters requesting the reports of Cooper's Hawk and Sharp-shinned Hawk sightings were distributed to four Arkansas State Parks, two USDA Forest Service offices and the Arkansas Natural Heritage Commission office in the spring of 1994. Second, the Arkansas Game and Fish Commission and three university ornithologists were contacted for information on the locations of historic nest sites of both species. Third, I arbitrarily selected forested areas that appeared to fit the habitat parameters described in the literature (Reynolds et al. 1982, Wiggers and Kritz 1991, Rosenfield and Bielefeldt 1993, Rosenfield et al. 1995) and searched them on foot for evidence of nesting accipiters.

The literature indicated that pine plantations and pure coniferous forests were used by accipiters, especially by Cooper's Hawks (Bosakowski et al. 1992a, 1992b). Therefore, most of the forest stands searched were pine plantations, but several deciduous stands were also examined. Each forest stand was first systematically searched using a Johnny Stewart Game Caller to broadcast calls of Cooper's Hawks and Great-horned Owls (*Bubo virginianus*) from roadsides or forest edges to solicit responses from potential nesting accipiters (Stewart et al. 1996, Rosenfield et al. 1985, Fuller and Mosher 1981). Calls were broadcast for approximately 20 sec followed by a 60-sec observation period, then repeated again. If an accipiter responded to the tape, it was followed if observed, or its approximate location was determined from vocalizations. If no responses were heard after approximately 5 min of

call broadcasting, the forest stand was systematically searched on foot to rule out the presence or absence of accipiters.

When nests were located, occupancy was verified by the presence or absence of adult hawks, freshly molted down or feathers, white wash (mutes) or young in the nest. If nest structures were considered to be unoccupied during the early part of the season, they were revisited later in the season to verify their status. If young had already hatched, the number of young and unhatched eggs were counted by climbing adjacent trees, or by using a telescoping pole and mirror to look into nests. Most nests were climbed when young were 12–14 d of age in order to determine nesting success and band them.

Habitat measurements were taken after the nestlings had reached fledging age (30–34 d) (Meng and Rosenfield 1988) or had left nests. The nest site was defined as a 10-m radius plot centered on the nest tree. Habitat variables such as canopy closure, canopy height and understory height were measured to define the vertical vegetative structure, while nest tree dbh, forest density (trees/ha) and understory density defined the horizontal vegetative structure (Table 1).

Accipiter and nest site data were analyzed using SPSS 5.0 programs. Two-tailed *t*-tests were conducted to determine any significant differences in habitat types between species. Between-group variance was tested using Levene's tests. Statistical significance was set at $P = 0.05$. A linear multiple regression model was developed for Cooper's Hawk nesting success using a three variable habitat model. The sample size for Sharp-shinned Hawks was too small to conduct a multiple regression analysis. However, Pearson correlation analyses were conducted between all variables to detect possible relationships within the samples for both species.

RESULTS

Searches for nesting Sharp-shinned and Cooper's Hawks were conducted in 48 forest stands. Seventy-nine percent of the stands searched were pine forests. They included exotic pine plantations (*Pinus taeda*) and uneven aged shortleaf pine forests (*P. echinata*). The remaining 21% of forests searched were deciduous (oak-hickory forests). These forest stands were distributed widely over 19 counties around the state (Fig. 1).

Four of the 12 occupied Cooper's Hawk nests (33%) were located using broadcasting calls. The other nest sites were found during thorough foot searches of forest stands. All of the Cooper's Hawk nest sites were located in loblolly pine plantations. These forest stands were of medium age (ca. 30–40 yr) and dense (>500 trees/ha) with moderately-dense understories (Table 2). All of the trees used by nesting Cooper's Hawks had diameters >25

¹ Present address: 179 CC 378, Bono, AR 72416 U.S.A.

Table 1. Habitat variables and methods used to characterize nest site habitat of Cooper’s and Sharp-shinned Hawks in Arkansas, 1994–96.

VARIABLE	PROCEDURE
Forest cover type	Species composition of overstory trees >75%
Forest density (trees/ha)	Number of trees counted within 10-m radius plot centered on the nest tree ^a
Percent canopy closure (%)	Horizontal density board grid (% covered)
Understory density	Index rating from 1–5 with 5 representing greatest density
Understory height (m)	Mean metric clinometer reading from four locations within the 10-m radius plot
Nest tree DBH (cm)	Diameter at breast height of nest tree
Nest tree height (m)	Metric clinometer reading 15 m from nest tree
Stand area (ha)	Measured from aerial photographs or GIS images ^b
Distance to nearest edge (m)	Shortest distance measured from nest tree to stand edge on ground
Distance to nearest water (m)	Shortest distance measured from nest tree to water ^c
Elevation (m)	Elevation of nest site taken from USGS 7.5 min topographic maps

^a Extrapolated to ha by no. of trees within 10 m radius/(3.14 × r²) × 10 000.
^b Used Mapix software GIS Landsat 5 imagery.
^c Measured using 100 m tape from nest tree to nearest visible water source. Could also be shortest distance to edge.

cm (\bar{x} = 31.2 cm; Table 2). Eighty-three percent of these nests were placed at the canopy base, while two were located well within the live foliage. Cooper’s Hawk nest sites were located at a mean elevation of 151.3 m (Table 2). Several nests were located in the same forest stand in consecutive years, but no evidence of returning individ-

uals was available. Therefore, each nest was considered an independent sample for habitat analysis.

One of the four Sharp-shinned Hawk nest sites (25%) was located after broadcasting Cooper’s Hawk calls and two were reported by individuals conducting songbird point counts in the Ozark National Forest during 1994. The remaining nest site was located by tracking screaming nestlings heard while searching a forest stand. All of the Sharp-shinned Hawk nest sites were located in uneven-aged, shortleaf pine stands with nest tree diameters ranging from 27.5–31.0 cm (\bar{x} = 29.3 cm). These stands ranged in density from 541–653 trees/ha (\bar{x} = 599.33 trees/ha) and understory densities were moderate (Table 2). The mean nest tree height was 22.0 m and the mean nest height was 18.4 m. All of the Sharp-shinned Hawk nests were placed approximately 1.5 m into the live foliage of nest trees. One of the nest structures was built on a limb 0.85 m from the main trunk while the other three were built next to the main trunk on one or more horizontal branches. Sharp-shinned Hawk nest sites were located at a mean elevation of 343.0 m (Table 2).

Mean forest density was significantly different between Cooper’s Hawks and Sharp-shinned Hawks (t = 4.41, P = 0.001; Table 2). Sharp-shinned Hawks were found only in the western part of the state at elevations significantly higher than Cooper’s Hawks (t = –5.53, P = 0.002; Fig. 1). Forest stand area (\bar{x} = 54.0 ha) for nesting Sharp-shinned Hawks was also significantly different than those of Cooper’s Hawks (\bar{x} = 10.2 ha, t = –9.23, P < 0.001). All other habitat variables were not significantly different between the two species (Table 2). Both species used nest sites that had moderate to high understory density (Cooper’s Hawk mean index = 3.17, Sharp-shinned Hawk mean index = 3.25), but understory height, while not significantly different, was shorter and slightly more dense at Sharp-shinned Hawk nest sites (Table 2).

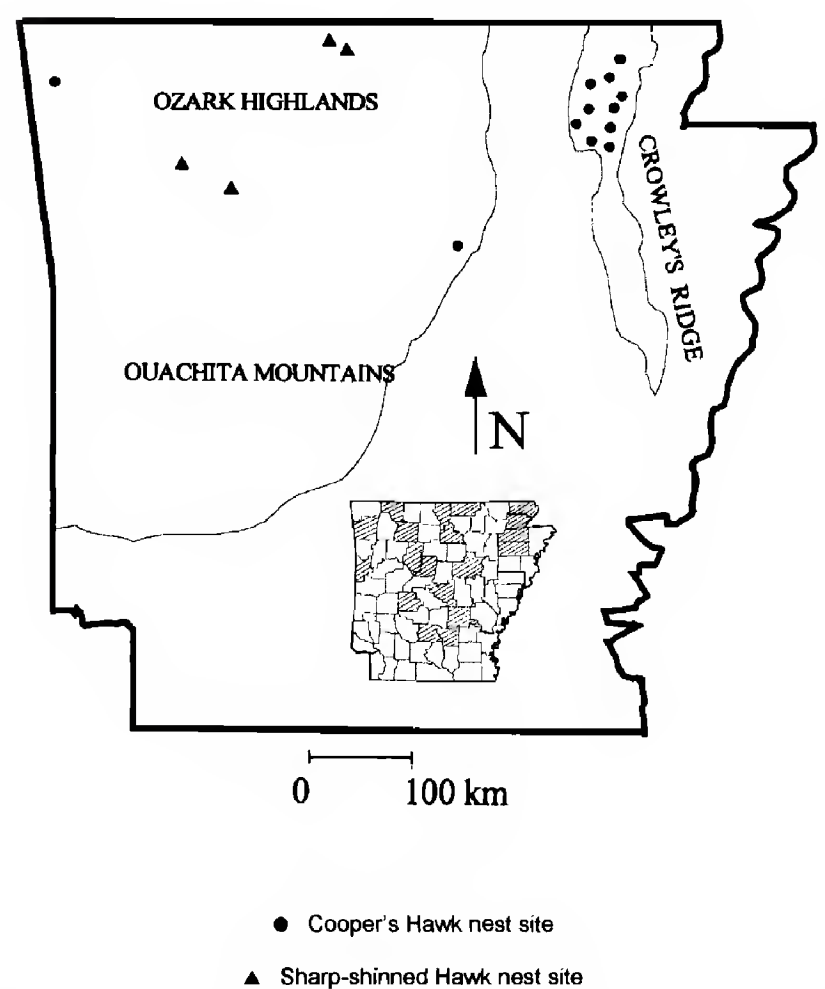


Figure 1. Map of Arkansas indicating counties searched (insert) and locations of Cooper’s and Sharp-shinned Hawk nest sites.

Table 2. Mean habitat measurements of Cooper’s (*N* = 12) and Sharp-shinned (*N* = 4) Hawk nest sites in Arkansas (1994–96).

HABITAT PARAMETERS	COOPER’S HAWK		SHARP-SHINNED HAWK		<i>P</i>
	\bar{x}	SE	\bar{x}	SE	
Forest density (trees/ha)*	935.7	69.0	599.3	32.4	0.001
Canopy closure (%)	71.3	1.52	62.5	6.6	0.280
Nest tree DBH (cm)	31.2	0.91	29.3	1.8	0.445
Nest tree height (m)	21.4	0.74	21.9	0.59	0.591
Nest height (m)	16.9	0.63	18.4	0.35	0.075
Understory density (1–4)	3.2	0.84	3.3	1.3	0.908
Distance to edge (m)	51.1	5.8	46.5	36.5	0.921
Distance to water (m)	145.6	36.5	47.5	37.5	0.145
Elevation (m)*	151.3	18.1	343.0	29.5	0.002
Forest stand area (ha)*	10.2	1.9	54.0	0.0001 ^a	0.000 ^b

* Significantly different between the two species (*P* ≤ 0.05).
^a Low sample size did not allow for accurate measure of standard error.
^b Low sample size did not allow for accurate measure of *P* value.

Pearson correlation analyses revealed several relationships between habitat variables and nesting success. Cooper’s Hawk nesting success improved with increased understory density and later hatch dates (*R* = 0.866, *P* = 0.005 for both correlations). In contrast, Sharp-shinned Hawk nesting success correlations increased with decreased understory density (*R* = −0.969, *P* = 0.031). Interestingly, Sharp-shinned Hawk nest height showed a negative correlation with increased elevation (*R* = − 0.999, *P* = 0.027). Cooper’s Hawk nest-site selection may have been influenced by available habitat, with nest height increasing with increased nest tree height (*R* = −0.654, *P* = 0.021). Cooper’s Hawk nesting habitat variables were entered into a multiple regression analysis with respect to nesting success. Habitat variables showing a relationship with nesting success were understory density, nest tree height and forest density (*R*² = 0.865, *F* = 8.51, *P* = 0.03).

DISCUSSION

Most of my search effort was focused in northeastern Arkansas. Therefore, more Cooper’s Hawk nest sites were located in that region. However, searches were conducted for both species in all stands visited around the state. Although one Cooper’s Hawk nest, which was unsuccessful, was found in the interior highlands of Arkansas, I felt that breeding Cooper’s Hawk densities were lower in that region, except where suitable forest fragmentation existed. Likewise, Sharp-shinned Hawks were only found in northern and western parts of the state, but I do not believe their range was restricted to that region. The small sample of Sharp-shinned Hawks limited statistical inferences about the distribution and habitat parameters used by this species.

The vertical structure of forest stands seemed to be a very important element in nest area use by Cooper’s

Hawks. All of the nest sites found had similar habitat variables with dominant trees reaching heights of over 20 m and understory species reaching heights of 10–12 m. The resulting space between the upper canopy base and understory may have served as a protective, horizontal corridor through the nest area. This may have reduced the visibility of nests to potential predators from above, such as Great Horned Owls (Rosenfield 1988).

Unlike the results of surveys by Reynolds et al. (1982) and Wiggers and Kritz (1991), Sharp-shinned Hawks in Arkansas nested in forests with tree densities up to 60% lower than nest stands of Cooper’s Hawks. Sharp-shinned Hawks also seemed to utilize uneven-aged and mature forest stands more than Cooper’s Hawks. This may have been due to the prey base of Sharp-shinned Hawks being more abundant in less dense forest stands with higher understory density. However, forests with similar structure and species composition were searched in lower elevations and no Sharp-shinned Hawks were detected. One other factor, stand size, may have played an important role in the distribution of accipiters. The interior highlands of Arkansas contain many large contiguous tracts of forested land with suitable songbird densities that may be more suitable for Sharp-shinned Hawks than Cooper’s Hawks. Likewise, the fragmented forests of eastern Arkansas (especially Crowley’s Ridge and the Ozark foothills) may provide more suitable nesting habitat and foraging edge for Cooper’s Hawks than Sharp-shinned Hawks.

RESUMEN.—Investigué un total de 48 parcelas de bosque entre 1994–96, incluyendo 38 de coníferas y 10 de bosques deciduos. Localizé 12 nidos ocupados de *Accipiter cooperii* y 4 de *Accipiter striatus*. Los nidos de *Accipiter striatus* fueron encontrados a alturas significativamente mayores en la parte oeste del estado, mientras que los de

Accipiter cooperii fueron encontrados en elevaciones menores en el noroccidente del estado. Todos los sitios de los nidos fueron localizados en bosques de pinos siendo los de *Accipiter cooperii* encontrados únicamente en plantaciones de *Pinus taeda*. Las variables de habitat fueron comparadas entre las dos especies con el fin de identificar diferencias potenciales en los habitats de anidación. El Porcentage de cobertura del dosel, la densidad de sotobosque, la altura del sotobosque, el diámetro del árbol del nido (dap), la altura del árbol del nido, la distancia al borde mas cercano fueron analizados. La distancia a la fuente de agua mas cercana no fue significativamente diferente entre las dos especies. Las variables de habitat que fueron significativamente diferentes incluyeron elevación y densidad del bosque en el área de las parcelas. El incremento en la densidad del sotobosque fue correlacionado con el éxito de anidación para *Accipiter cooperii* ($R = 0.866$, $P = 0.005$) y para *Accipiter striatus* ($R = -0.969$, $P = 0.031$).

[Traducción de César Márquez]

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LITERATURE CITED

- BOSAKOWSKI, T., D.G. SMITH AND R. SPEISER. 1992a. Niche overlap of two sympatric-nesting hawks *Accipiter* spp. in the New Jersey-New York Highlands. *Ecography* 15: 358-372.
- , ——— AND ———. 1992b. Nest sites and habitat selected by Cooper's Hawks, *Accipiter cooperii*, in northern New Jersey and southeastern New York. *Can. Field-Nat.* 106:474-479.
- FULLER, M.R. AND J.A. MOSHER. 1981. Methods of detecting and counting raptors: a review. Pages 235-246 in C.J. Ralph and J.M. Scott [EDS.], Estimating numbers of terrestrial birds. *Stud. Avian Biol.* 6.
- JAMES, A.D. AND J.C. NEAL. 1986. Arkansas birds, their distribution and abundance. Univ. Arkansas Press, Fayetteville, AR U.S.A.
- MENG, H.K. AND R.N. ROSENFELD. 1988. Cooper's Hawk: reproduction. Pages 331-349 in R.S. Palmer [ED.], Handbook of North American birds, Vol. 4, Part 1: diurnal raptors. Yale Univ. Press, New Haven, CT U.S.A.
- REYNOLDS, R.T., E.C. MESLOW AND H.M. WIGHT. 1982. Nesting habitat of coexisting *Accipiter* in Oregon. *J. Wildl. Manage.* 46:124-137.
- ROSENFELD, R.N. AND J. BIELEFELDT. 1993. Cooper's Hawk (*Accipiter cooperii*). In A. Poole and F. Gill [EDS.], The birds of North America, No. 75. The Academy of Natural Sciences, Philadelphia, PA and The American Ornithologists' Union, Washington, DC U.S.A.
- , J. BIELEFELDT, J.L. AFFELDT AND D.J. BECKMANN. 1995. Nesting density, nest area reoccupancy, and monitoring implications for Cooper's Hawks in Wisconsin. *J. Raptor Res.* 29:1-4.
- , ——— AND W.A. ANDERSON. 1985. Taped calls as an aid in locating Cooper's Hawk nests. *Wildl. Soc. Bull.* 13:62-63.
- STEWART, A.C., R.W. CAMPBELL AND S. DICKIN. 1996. Use of dawn vocalizations for detecting breeding Cooper's Hawks in an urban environment. *Wildl. Soc. Bull.* 24: 291-293.
- WIGGERS, E.P. AND K.J. KRITZ. 1991. Comparison of nesting habitat of coexisting Sharp-shinned Hawks and Cooper's Hawks in Missouri. *Wilson Bull.* 103:568-577.

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PREDATION ON MEXICAN FREE-TAILED BATS BY BURROWING OWLS IN CALIFORNIA

GEOFFREY M. HOETKER AND KENNETH W. GOBALET

Department of Biology, California State University, Bakersfield, Bakersfield, CA 93311 U.S.A.

KEY WORDS: *Burrowing Owl*; *Athene cunicularia*; *Mexican free-tailed bat*; *Tadarida brasiliensis*; *predation*.

The Burrowing Owl (*Athene cunicularia*) is opportunistic in its feeding habits (Thomsen 1971, Zarn 1974, Snyder and Wiley 1976) and the abundance of items found in its pellets may be a reflection of relative prey availability (Glover 1953, Thomsen 1971, Gleason and Craig 1979). Among insect prey, Burrowing Owls primarily consume crickets, grasshoppers, ground beetles and dragonflies (Bent 1938, Glover 1953, Thomsen 1971). Small rodents such as meadow voles (*Microtus* spp.), deer mice (*Peromyscus* spp.), house mice (*Mus musculus*), pocket mice (*Perognathus* spp.), harvest mice (*Reithrodontomys* spp.), pocket gophers (*Thomomys* spp.) and kangaroo rats (*Dipodomys* spp.) are also typical food items (Earhart and Johnson 1970, Gleason and Craig 1979, Conroy and Chesemore 1987, Haug and Oliphant 1990). Burrowing Owls will also eat birds, including Horned Larks (*Eremophila alpestris*), Western Meadowlarks (*Sturnella neglecta*), Red-winged (*Agelaius phoeniceus*) or Brewer's Blackbirds (*Euphagus cyanocephalus*) and various shorebirds (Errington and Bennet 1935, Bent 1938, Thomsen 1971, Gleason and Craig 1979).

Occasionally, unexpected prey are found in Burrowing Owl pellets. Numerous remains of spadefoot toads (*Scaphiopus* spp.) were found in pellets in Kansas (Sperry 1941) and Nevada (Bond 1942). Crayfish (*Cambarus* spp.) were the most common food items in a Colorado study (Hamilton 1941) and attacks on large snakes have also been documented (Fisher 1893).

Despite the potential to feed on whatever prey are readily available, there have been few reports of Burrowing Owls feeding on bats. Conroy and Chesemore (1987) discovered the remains of at least 13 mammalian species, but no bats in 963 Burrowing Owl pellets collected in Fresno County, California. Thomsen (1971) discovered the remains of a single hoary bat (*Lasiurus cinereus*) in 2112 pellets collected from a colony of Burrowing Owls in Alameda County, California. Bent (1938), in a list of potential mammalian prey of Burrowing Owls, vaguely mentioned bats only as a possible prey source. Upon examination and analysis of Burrowing Owl pellets collected in April 1989, we found numerous bat skeletal remains. This study presents evidence of Burrowing Owl predation on Mexican free-tailed bats (*Tadarida brasiliensis*) in Bakersfield, California.

MATERIALS AND METHODS

A pair of Burrowing Owls were observed for 2 wk in April 1989. A total of 18 pellets was collected from the vicinity of the burrow and from perches used by the owls in an undeveloped urban field in Bakersfield, California. Vertebrate remains were identified to species using diagnostic bone fragments including maxillae, dentaries, pelvises, limbs and vertebrae. The number of individual prey items found in an individual pellet was based on the maximum number of single, paired or vertebral elements that can exist in a single individual. Insect remains were identified to order but not quantified. All vertebrate identifications were based on comparisons with skeletons in the collection housed in the Department of Biology, California State University, Bakersfield. Though the precise species of bat caught is likely insignificant, identification criteria are included to assist in future studies.

House mice were identified by their dentition and western toads (*Bufo boreas*) by the size and shape of their vertebrae. Teeth were commonly missing from bat dentaries. In such cases, we based identifications on skeletal characters. Three similar species of small bats inhabit this area of California: the Mexican free-tailed bat, Yuma myotis (*Myotis yumanensis*) and long-eared myotis (*M. evotis*). The remains of these three species of small bats can be distinguished by dentaries. The Mexican free-tailed bat possesses five post-canine teeth, whereas the Yuma myotis and the long-eared myotis possess six. In *Myotis*, the mental foramen is ventral to the canine and the coronoid process is low, rounded and only slightly elevated above the mandibular condyle, whereas in the Mexican free-tailed bat, the mental foramen is ventral to the first premolar and the coronoid is pointed, tapered and narrow, extending well above the condyle. The angular process of the Mexican free-tailed bat is blunt and rounded, whereas in *Myotis* it is sharply pointed and tapers caudally. Additionally, the zygomatic arch of the Mexican free-tailed bat is much broader dorsoventrally than in *Myotis*. The Mexican free-tailed bat also bears a dorsoventrally oriented preorbital ridge that is lacking in *Myotis*, and its epipubic process is elongate and pointed rather than rounded and short as in *Myotis*.

RESULTS AND DISCUSSION

In the 18 Burrowing Owl pellets collected, the dominant vertebrate prey item was the Mexican free-tailed bat (Table 1). Remains of at least 28 vertebrates were found, of which 20 (71%) were bats. One pellet contained the remains of at least four bats, another pellet contained at least three. Other vertebrate prey consisted of western toads and house mice. Two of the pellets contained non-

Table 1. Vertebrate prey found in 18 pellets from a pair of Burrowing Owls in Bakersfield, California (April 1989), including minimum number of individuals and number of pellets in which they appeared.

TAXON	MINIMUM NUMBER OF INDIVIDUALS	NUMBER OF PELLETS
Mexican free-tailed bat	20	12
House mouse	3	3
Western toad	3	3
Unidentified rodents	2	2

diagnostic small rodent-sized bones, whereas insect material (primarily coleopteran and orthopteran) was found in almost all pellets.

Although this is the first study that documents consumption of bats by Burrowing Owls, other raptors including the Great Horned Owl (*Bubo virginianus*), Barn Owl (*Tyto alba*), Cooper’s Hawk (*Accipiter cooperii*), Sharpshinned hawk (*A. striatus*), Swainson’s Hawk (*Buteo swainsoni*), Red-tailed Hawk (*B. jamaicensis*), Northern Harrier (*Circus cyaneus*), American Kestrel (*Falco sparverius*) and Peregrine Falcon (*F. peregrinus*) have been found to feed on bats (Twente 1954, Baker 1962, Byre 1990). Baker (1962) reported that Great Horned Owl pellets from Carlsbad Caverns National Park in New Mexico were composed almost entirely of Mexican free-tailed bat bones and fur. Barn Owls have been observed to prey upon Mexican free-tailed bats exiting caves in Oklahoma (Twente 1954). In northeastern Illinois, Peregrine Falcons intercepted individuals of three species of bats (silver-haired, *Lasionycteris noctivagans*; big brown, *Eptesicus fuscus*; and red, *Lasiurus borealis* bats) migrating across Lake Michigan during the early morning (Byre 1990).

Upon exiting their roosts, usually in great numbers, bats can be extremely vulnerable to nocturnal avian predators (Baker 1962). Congregations of some bat species have been observed in the evening around artificial lighting. In accordance with large aggregations of potential prey, Burrowing Owls in our study may have hunted near artificial light sources several hundred meters from their burrow. For example, in 1997 at a separate location, a Burrowing Owl was seen repeatedly attacking a bat flying around a lightpost in a shopping mall parking lot. At the time of our study, numerous businesses, residential buildings and other structures suitable for roosting were within a few hundred meters of the burrow. Although these sites were not searched for roosts in April 1989 when the pellets were collected, any such structures are potential havens for groups of bats (Hall and Kelson 1959, Walker 1975, Barclay et al. 1980, Kunz 1982, Jameson and Peeters 1988, Thomas and LaVal 1988). These sites were well within the limits of known home ranges (≤ 3.43 km²) of Burrowing Owls (Haug and Oliphant 1990), and could

have provided an opportunity for predation close to the bats’ roost(s).

Our results provide evidence that, for at least two weeks, the owls were opportunistic, nocturnal predators taking advantage of an accessible supply of bats. In other localities in Bakersfield, accumulations of western toad carcasses have been found associated with Burrowing Owl burrows, or pellets have been packed with insect parts (pers. obs.). Bat roosts were most likely in buildings close to the owls’ burrow.

RESUMEN.—Un análisis de 18 egragópilas de *Athene cunicularia* reveló que la presa vertebrado dominante fue *Tadarida brasiliensis*. Las egragópilas fueron recolectadas durante un período de dos semanas en abril de 1989 en un área urbana de Bakersfield, California. Esta es la primera documentación de depredación de murciélagos por *Athene cunicularia*. Otros restos identificables de vertebrados en las egragópilas incluyeron a *Bufo boreas* y *Mus musculus* [Traducción de César Márquez]

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LITERATURE CITED

BAKER, J.K. 1962. The manner and efficiency of raptor depredation on bats. *Condor* 64:500–504.

BARCLAY, R.M.R., D.W. THOMAS AND M.B. FENTON. 1980. Comparison of methods used for controlling bats in buildings. *J. Wildl. Manage.* 44:502–506.

BENT, A.C. 1938. Life histories of North American birds of prey. Part 2. Smithsonian Inst. U.S. Natl. Mus. Bull 170, Washington, DC U.S.A.

BOND, R.M. 1942. Food of the Burrowing Owl in western Nevada. *Condor* 44:183.

BYRE, V.J. 1990. A group of young Peregrine Falcons prey on migrating bats. *Wilson Bull.* 102:728–730.

CONROY, R.M. AND D.L. CHESEMORE. 1987. Food habits of the Burrowing Owl (*Athene cunicularia*) in Fresno County, California. Pages 105–110 in D.F. Williams, S. Byrne and T.A. Rado [Eds.], *Endangered and sensitive species of the San Joaquin Valley, California: their biology, management, and conservation*. California Energy Commission, Sacramento, CA U.S.A.

EARHART, C.M. AND N.K. JOHNSON. 1970. Size dimorphism and food habits of North American owls. *Condor* 72:251–264.

ERRINGTON, P.L. AND L.J. BENNET. 1935. Food habits of Burrowing Owls in northwestern Iowa. *Wilson Bull.* 47: 125–128.

FISHER, A.K. 1893. The hawks and owls of the United States in their relation to agriculture. USDA, Div. Ornithol. and Mammal. Bull. 3.

- GLEASON, R.L. AND T.H. CRAIG. 1979. Food habits of Burrowing Owls in southeastern Idaho. *Great Basin Nat.* 39:274-276.
- GLOVER, F.A. 1953. Summer foods of the Burrowing Owl. *Condor* 55:275.
- HALL, E.R. AND K.R. KELSON. 1959. The mammals of North America. Vol. 1. Ronald Press, New York, NY U.S.A.
- HAMILTON, W.J. 1941. A note on the food of the western Burrowing Owl. *Condor* 3:74.
- HAUG, E.A. AND L.W. OLIPHANT. 1990. Movements, activity patterns, and habitat use of Burrowing Owls in Saskatchewan. *J. Wildl. Manage.* 54:27-35.
- JAMESON, E.W. AND H.J. PEETERS. 1988. California mammals. Univ. California Press, Berkeley, CA U.S.A.
- KUNZ, T.H. 1982. Roosting ecology of bats. Pages 1-55 in T.H. Kunz [ED.], *Ecology of bats*. Plenum Press, New York, NY U.S.A.
- SNYDER, N.F.R. AND J.W. WILEY. 1976. Sexual size dimorphism in hawks and owls of North America. *Ornithol Monogr.* No. 20.
- SPERRY, C.C. 1941. Burrowing Owls eat spadefoot toads. *Wilson Bull.* 53:45.
- THOMAS, D.W. AND R.K. LAVAL. 1988. Survey and census methods. Pages 77-89 in T.H. Kunz [ED.], *Ecological and behavioral methods for the study of bats*. Smithsonian Institution Press, Washington, DC U.S.A.
- THOMSEN, L. 1971. Behavior and ecology of Burrowing Owls on Oakland Municipal Airport. *Condor* 73:177-192.
- TWENTE, J.W. 1954. Predation on bats by hawks and owls. *Wilson Bull.* 66:135-136.
- WALKER, E.P. 1975. Mammals of the world. Vol. 1. Johns Hopkins Univ. Press, Baltimore, MD U.S.A.
- ZARN, M. 1974. Habitat management series for unique or endangered species: Burrowing Owl. USDI/BLM. Denver Service Center, Tech. Note 250, Report 11

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NEAREST NEIGHBOR NEST DISTANCES, HOME RANGE AND TERRITORY AREA OF THE MADAGASCAR FISH-EAGLE (*HALIAEETUS VOCIFEROIDES*)

RICHARD T. WATSON

The Peregrine Fund, 566 West Flying Hawk Lane, Boise, ID 83709 U.S.A.

SUZANNE RAZAFINDRAMANANA

Ankoay Trust for Conservation, B.P. 4113, Antananarivo (101), Madagascar

KEY WORDS: *Madagascar Fish-Eagle*, *Haliaeetus vociferoides*; carrying capacity; conservation; ecotone; endangered; spatial utilization.

The Madagascar Fish-Eagle (*Haliaeetus vociferoides*) is endemic to Madagascar and considered endangered due to its low and declining population of only 100-120 breeding pairs (Langrand and Meyburg 1989, Colar et al. 1994, Rabarisoa et al. 1997). Little was known about the species' biology or ecology until intensive studies began in 1991 aimed at understanding its natural history, with emphasis on those ecological parameters that may influence survival and to suggest a design for a conservation recovery program (Watson 1997).

The area needed to support a breeding pair of eagles is an important ecological parameter that can determine the carrying capacity of suitable habitat (Newton 1979), and can be estimated from measurement of

nesting density, nearest neighbor nest distance, home range area or territory area. In continuous suitable habitat, noncolonial nesting raptors generally space themselves by maintaining a mutually exclusive territory which pairs defend by a variety of behavioral displays and interactions (Newton 1979). Nearest neighbor distances can be used to estimate nest spacing in species that nest only along linear ecotones, such as the Madagascar Fish-Eagle which nests only along woodland to water ecotones. An estimate of pair spacing can be used to extrapolate population carrying capacity if the area of suitable habitat is known, carrying capacity being an important estimate for setting a target population size for endangered species recovery. In this report, we evaluate the relative suitability of nearest neighbor nest distance, home range and territory size as indices of the area needed to support a pair of eagles and their use in estimating the Madagascar Fish-Eagle population carrying capacity.

Table 1. Home range parameters of six adjacent Madagascar Fish Eagle pairs on three adjacent lakes in western Madagascar in 1993.

PAIR NAME (PAIR NO.)	NO. OF OBSERVATIONS	MAX. AREA (ha)	90%- PROBABILITY (ha)	50%- PROBABILITY (ha)	NOTES
Befo-2 (3)	245	266	154	9.4	nest on island
Befo-3 (4)	403	244	44	0.3	
Soam-2 (24)	396	487	292	3.2	
Soam-1 (1)	333	434	224	6.7	
Mean		350	189	8.1	
SD		118.8	49.5	1.9	

METHODS

Nearest neighbor nest distances and intra-pair alternate nests were measured during the breeding period (June–October) each year from 1992–96 at three adjacent lakes (Lakes Ankerika, Befotaka and Soamalipo) in western Madagascar. The study area was thoroughly surveyed at the start of each breeding season to find every breeding pair. Nest sites were marked on a 1:40 000 scale map from which distance measurements were made. Nearest neighbor nest distances included only those pairs that built or repaired nests within the year of measurement.

In 1993, we made behavioral observations of four adjacent nesting pairs to measure home range and territory size. Home range was defined as that area used by pair members for any activity. Territory size was defined as that area defended by the pair, either by aggressive intraspecific interactions with intruders or by prominent displays and duetting calls by the pair. Daily observations took place from dawn to midday or from midday to dusk once per week at each of the nests for the duration of the breeding period. Members of the focal pair were tracked visually for as long as possible by two mobile observers who worked together on foot or by boat to keep birds in sight. Each new position of a bird was recorded on a 1:40 000 map of the lakes overlaid with a 40 × 40 m grid. Individual birds were recognized by radio tags, leg bands and/or visits to their own nest site. Sexes were differentiated by the relatively larger size of the female and the lower pitch of her vocalizations. Territory and home range size were calculated from subsampled independent observations using Ranges IV (Biotrack, U.K.) to determine the minimum-area convex polygon size, and 90%- and 50%-probability areas (Kenward 1987).

RESULTS

Pairs used a mean of 3.5 alternate nests in the five year study period. One pair (Befo-3) moved to alternate nests each year and built a total of six nests during the study, while others (e.g., Anke-1) used the same nest for up to three successive years. Pairs moved to alternate nests in 28 of the 36 pair-years recorded, a 78% relocation rate. Because pairs moved to alternate nests, nearest neighbor nest distances changed every year.

The mean distance between alternate nests for all pairs over all years was 0.54 ± 0.49 km (±SD). Although the center of activity of pairs tended to remain more or less constant, two pairs moved to alternate nests 1.9 and 2.3 km from their previous nests and made large changes in center of activity. Although these figures reflected distances between alternate nests used in successive years, Madagascar Fish-Eagles were observed to construct or reconstruct more than one nest during the prebreeding season, eventually settling on one for the year’s breeding attempt.

The mean nearest neighbor nest distance for each year was: 1.55 ± 0.30 km in 1992 (N = 10), 1.80 ± 0.35 km in 1993 (N = 9), 1.58 ± 0.56 km in 1994 (N = 11), 1.55 ± 0.56 km in 1995 (N = 10) and 1.94 ± 1.13 km in 1996 (N = 9). The mean nearest neighbor nest distance for all years was 1.68 ± 0.66 km (N = 49). Although most nearest neighbors were at fairly consistent distances from each other, one pair, Befo-2, moved its nest site 2.3 km to another small lake in 1996, where its nearest neighbor was on Lake Befotaka nearly 5 km away.

Maximum home ranges for four adjacent fish eagle pairs on Lakes Befotaka and Soamalipo in 1993 ranged from 244–487 ha, with a mean of 350 ha ± 119 ha (Table 1). The mean 90%-probability range was 189 ha indicating that about 54% of the maximum range was created by infrequent visits by fish eagles to distant points in the range. The 90%- or 50%-probability ranges were therefore more useful figures for making comparisons of range size between pairs, years or seasons. One pair, Befo-3, had a substantially smaller range size, especially when comparing the 90%- and 50%-probability ranges between pairs (Table 1). This was most likely because Befo-3 nested on an island which offered more abundant access to aquatic and shoreline habitats. The difference was still apparent, but not so great, even when considering the maximum home range size which included occasional long forays across the lake to opposite shores.

Territory size varied considerably from 24–273 ha with a mean of 116 ± 80.6 ha (Table 2), the smallest

Table 2. Territory size of four adjacent Madagascar Fish Eagle pairs on Lakes Befotaka and Soamalipo in 1993.

PAIR NAME (PAIR NO.)	NO. OF OBSERVA- TIONS	MAX. AREA (ha)	90%- PROBABILITY AREA (ha)	50%- PROBABILITY AREA (ha)	NOTES
Befo-2 (3)	21	59	19	4.7	nested on island
Befo-3 (4)	71	24	2.7	0.2	
Soam-2 (24)	65	273	203	1.2	
Soam-1 (1)	74	173	117	4.9	
Mean		116	68	4.8	
SD		80.6	69.3	0.14	

territory being that of the island nesting pair. The large variation in territory size between these four pairs remained evident even when comparing 90%- and 50%-probability areas (Table 2), suggesting that territory size was consistent within each pair. We speculated that differences in territory size reflected differences between the visibility of interlopers and/or the audibility of territorial vocalizations, both associated with the physical characteristics of the territory (e.g., relative proportions of forest to open water). We saw no physical interactions between neighboring pairs. Intraspecific interactions were recorded only between resident birds and conspecifics that came from outside the study area and were not recognized as neighbors. It appeared that territories were recognized by neighbors and were maintained without physical interaction by calling and perching in a prominent location.

DISCUSSION

The Madagascar Fish-Eagle’s maximum home range varied by nearly 100% and even the mean 90%-probability range varied by a factor of six times (from 44–292 ha). In any case, home range was a poor measure of carrying capacity because of the likelihood of shared foraging areas with neighboring pairs. Territory size was likely not a useful parameter for extrapolations of carrying capacity either. In the case of the Madagascar Fish-Eagle, where territory was maintained largely by visual and audible displays that carried over a large distance, measurements based on the residents’ location was probably not an accurate reflection of actual territory size.

We concluded that nearest neighbor nest distances were the best source of estimation. In the case of the Madagascar Fish-Eagle, they were much less variable and consistent with the linear nature of suitable nesting habitat (i.e., woodland to water ecotones). Thus, they offered a direct way of estimating overall carrying capacity in areas of known suitable habitat.

RESUMEN.—Los estudios de comportamiento fueron conducidos desde 1992–96 para medir la variación en la utilización espacial de la amenazada águila pesca-

dora de Madagascar. Los resultados mostraron que la media de la distancia del nido vecino mas cercano fue de 1.68 ± 0.66 km (\pm SD), la media de la distancia al nido alterno fue de 0.54 ± 0.49 km y el centro de actividad de las parejas fue mas o menos constante. El rango del hogar máximo de 4 parejas oscilo entre 244–487 ha, con una media de 350 ± 119 ha. La media 90% de probabilidad de rango de hogar fue de 189 ha. El tamaño del territorio varió considerablemente de 24–273 ha con una media de 116 ± 80.6 ha. El rango y territorio de una pareja anidando en el interior de la isla fue substancialmente mas pequeño que el de otras. Los estimativos del tamaño del territorio fueron muy variables para ser utilizados y poder estimar la capacidad de carga de habitats convenientes. La distancia del nido vecino mas cercano fue mucho menos variable, dado que es una medida linear consistente con la naturaleza del habitat de anidación consistente para el águila pescadora (i.e., ecotonos de bosques y acuáticos) decidimos considerar esta como el mejor parametro para estimar la capacidad de carga en habitats convenientes.

[Traducción de César Márquez]

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LITERATURE CITED

COLLAR, N.J., M.J. COSBY AND A.J. STATTERSFIELD. 1994. Birds to watch 2. BirdLife International, Cambridge, U.K.

KENWARD, R. 1987. Wildlife radio tagging. Academic Press, San Diego, CA U.S.A.

LANGRAND, O. AND B.-U. MEYBURG. 1989. Range, status and biology of the Madagascar Sea-Eagle (*Haliaeetus vociferoides*). Raptors in the modern world. WWGBP Berlin, Germany.

- NEWTON, I. 1979. Population ecology of raptors. Buteo Books. Vermillion, SD U.S.A.
- RABARISOA, R., R.T. WATSON, R. THORSTROM AND J. BERKLEMAN. 1997. Status of the Madagascar Fish-Eagle *Haliaeetus vociferoides* in 1995. *Ostrich* 68:8–12.
- WATSON, R.T. [ED.]. 1997. Madagascar wetlands conservation project. Progress Report III, 1995–1996. The Peregrine Fund, Boise, ID U.S.A.

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DUMPS FOR DEAD LIVESTOCK AND THE CONSERVATION OF WINTERING RED KITES (*MILVUS MILVUS*)

DAVID SERRANO LARRAZ

Department of Applied Biology, Estación Biológica de Doñana, Pabellón del Perú, Avenida de María Luisa s/n,
41013 Sevilla, Spain

KEY WORDS: conservation; diet; *Milvus milvus*; dead livestock; wintering populations.

The main European population of Red Kites (*Milvus milvus*) winters in Spain (Viñuela 1996), where management of this species is critical for its conservation. Red Kites usually feed on carrion (Cramp 1980) and refuse and carrion disposal sites may be important winter feeding areas (García et al. 1998). In this paper, I evaluate the importance of livestock carcass disposal sites for kites in the Ebro Valley, which, together with the northern plateau, is one of the most important wintering areas in Spain (De Juana et al. 1988, Sunyer and Viñuela 1996).

STUDY AREA AND METHODS

The study area was in the semiarid Mediterranean basin that is crossed by the Ebro River in northeastern Spain (Zaragoza and Huesca Provinces, 41°39'N, 00°54'W). Diet composition was studied by analysis of pellets collected in communal roosts that were used by most of the wintering population. This kind of analysis allowed me to infer indirectly the foraging habits of the birds, avoiding more costly techniques such as radiotracking.

I visited three of the most important roosts situated in the two main landscape types in this area: roosts Almudévar and Leciñena were in dry lands (nonirrigated crops) and roost Luceni was in irrigated land near the Ebro River. In 1993, the number of Red Kites roosting at these three locations were 60, 75 and 90, respectively (SEO-Aragón 1994), remaining roughly constant during the study period. At the Almudévar roost, pellets were collected at the end of February 1996 and reflected the winter diet. Leciñena and Luceni roosts were visited in November 1997 and reflected the autumn diet. Pellets were collected in the morning, when all the kites had left the roosts to avoid disturbance. Prey analyses were made according to Blanco et al. (1990), assuming that one kite consumed 95 g of food and regurgitated one pellet per

day. When the weight of one prey item in a pellet was heavier than this amount (e.g., a rabbit), we assumed that 95 g of prey had been consumed. When a pellet was composed of prey of lesser biomass, their partial contributions were added. When a pellet was composed of both prey over 95 g and prey of lesser biomass, we subtracted the weights of small prey from 95 g and added this amount to the heavier one. This method has been shown to accurately estimate diet composition in kites (Blanco et al. 1990). All prey weights were obtained from the literature. Prey were grouped in the following six categories: domestic animals (poultry, domestic rabbits and sheep), wild rabbits (*Oryctolagus cuniculus*) and hares (*Lepus granatensis*), small rodents, wild birds, reptiles and insects.

RESULTS

A total of 1892 food items were identified among the 262 pellets analyzed (Table 1). The most important food item in terms of biomass was carrion of domestic animals. Poultry and domestic rabbits made up >80% of the domestic-prey biomass, although other types of prey, such as small rodents and wild rabbits, were also important. Carrion of domestic animals and small rodents made up at least 60% of the biomass at the three roosts. On the Spanish northern plateau, carrion of small domestic animals has also been reported to be the main food of Red Kites but fluctuations in diet composition occur with cyclic fluctuations in numbers of common voles (*Microtus arvalis*) (Sunyer and Viñuela 1994, García et al. 1998). The high numerical importance of small rodents in my study could have also been related to the temporary abundance of voles (*Pitymys duodecimcostatus*), which made up 62% of the rodents consumed. High numbers of insects in the diet in autumn were probably associated with the massive emergence of flying ants which reached 85% of the total insect prey.

Table 1. Diet of the Red Kite at three roost sites in the mid-Ebro Valley, Spain.

	ROOST SITES					
	ALMUDÉVAR		LUCENI		LECIÑENA	
	%n ^a	%b ^b	%n	%b	%n	%b
Carrion	23.7	39.7	5.9	53.9	8.9	43.4
Wild lagomorphs	18.4	31.1	—	—	1.1	5
Rodents	38.2	20.4	12.1	32.3	21	42.1
Wild birds	7.2	8.7	1.4	7.2	1.2	4.3
Reptiles	—	—	—	—	0.1	0.6
Insects	12.5	0.1	80.6	6.6	67.7	4.6
Total prey items	152		861		879	
Total pellets	67		83		112	

^a Percent of prey items.
^b Percent of prey biomass.

Small livestock carcasses were mainly in dumps (Tella 1993). My data show the significance of these sites as food sources for Red Kites and concur with previous findings on the northern plateau (García et al. 1998). In other localities with fewer wintering kites, they mainly made use of alternative food sources such as game species and other wild animals (Blanco et al. 1990, Ortega and Casado 1991, García et al. 1998). Possibly, the use of predictable, localized carrion in dumps resulted in greater winter survival of kites (Donázar 1992) and the large number of wintering kites at carrion dumps. Owing to the fluctuations in vole numbers in Mediterranean areas of Europe, this human-related food source seems critical for some wintering populations of kites.

Some studies have shown the importance of maintaining traditional dumps for dead livestock (muladares) and refuse sites for the conservation of several species of threatened, scavenging raptors (Fernández 1990, Donázar 1992, Tella 1993, Donázar et al. 1996, Blanco 1997). Currently, sanitation regulations in Spain forbid leaving dead domestic animals in the field and management of dumps for dead livestock and refuse pits prevents raptors from exploiting them as feeding sites because carcasses are buried or dumped in ditches (Sampietro et al. 1997). These regulations are clearly discordant with the conservation of scavenger raptors whose populations are declining. Therefore, it is necessary to achieve better compatibility between health laws and wildlife preservation laws.

RESUMEN.—Se estudia la dieta otoñal e invernal del milano real (*Milvus milvus*) en el valle del Ebro (Aragón, NE España), una de las zonas más importantes para la invernada de la especie de toda Europa. Fueron analizadas 262 egagrópilas recogidas en tres de los dormideros más importantes del área de estudio sumando un total de 1892 presas. Carroña de pequeños animales domésticos (conejos y pollos de granja) y micromamíferos (arvicóli-

dos principalmente) totalizaron al menos el 60% de la biomasa en los tres dormideros. Otras presas importantes en frecuencia de captura fueron lagomorfos silvestres en invierno e insectos en la dieta otoñal. Dado que la mayor parte de los pequeños animales domésticos son vertidos en muladares en el área de estudio, se pone de manifiesto la importancia de estos puntos para la conservación europea de la especie, sobre todo teniendo en cuenta que las leyes zoosanitarias en España son claramente incompatibles con la conservación de especies de aves rapaces carroñeras amenazadas.
[Traducción de Autor]

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LITERATURE CITED

BLANCO, G. 1997. Role of refuse as food for migrant, floater and breeding Black Kites (*Milvus migrans*). *J Raptor Res.* 31:71–76.
———, F. HIRALDO AND B. HEREDIA. 1990. Variations in the diet and foraging behavior of a wintering Red Kite (*Milvus milvus*) population in response to changes in food availability. *Ardeola* 37:267–278.
CRAMP, S. 1980. The birds of the western Palearctic. Vol 2. Academic Press, London, U.K.
DE JUANA, E., F. DE JUANA AND S. CALVO. 1988. La invernada de las aves de presa (O. Falconiformes) en la Península Ibérica. Pages 97–122 in J.L. Tellería [ED.], Invernada de aves en la Península Ibérica. Monografía No. 1., SEO-BirdLife, Madrid, Spain.
DONÁZAR, J.A. 1992. Muladares y basureros en la biología y conservación de las aves en España. *Ardeola* 39:29–40.
———, O. CEBALLOS AND J.L. TELLA. 1996. Communal roosts of Egyptian Vultures (*Neophron percnopterus*): dynamics and implications for the species conservation. Pages 189–201 in J. Muntaner and J. Mayol [EDS], Biology and conservation of Mediterranean raptors, 1994. Monografía No. 4. SEO-BirdLife, Madrid, Spain.
FERNÁNDEZ, C. 1990. Importancia de los muladares en la alimentación de los buitres. *Quercus* 50:11–17.
GARCÍA, J.T., J. VIÑUELA AND C. SUNYER. 1998. Geographic variation of the winter diet of the Red Kite *Milvus milvus* in the Iberian Peninsula. *Ibis* 140:302–309.
ORTEGA, A. AND S. CASADO. 1991. Alimentación del milano real *Milvus milvus* en la provincia de Madrid. *Doñana Acta Vertebrata* 18:195–204.
SAMPIETRO, F.J., E. PELAYO AND M. CABRERA. 1997. La importancia de los muladares en la conservación de las rapaces carroñeras en Aragón. *Quercus* 137:18–22.
SEO-ARAGÓN. 1994. Anuario ornitológico de Aragón. Zaragoza, Spain.
SUNYER, C. AND J. VIÑUELA. 1994. Variación temporal en

los hábitos alimentarios del milano real durante la invernada en la Meseta Norte. *Ardeola* 41:161–167.

- AND ———. 1996. Invernada de rapaces (O. Falconiformes) en España peninsular e Islas Baleares. Pages 361–370 in J. Muntaner and J. Mayol [EDS.], *Biology and conservation of Mediterranean raptors*, 1994. Monografía No. 4. SEO-BirdLife, Madrid, Spain.
- TELLA, J.L. 1993. Inventariado de los muladares y la valoración de su importancia para el Alimoche (*Neophron percnopterus*) en el valle Medio del Ebro. Servicio Provincial de Agricultura, Ganadería y Montes. Diputación General de Aragón, Zaragoza, Spain.

- VIÑUELA, J. 1996. Situación del milano real (*Milvus milvus*) en el Mediterráneo. Pages 91–100 in J. Muntaner and J. Mayol [EDS.], *Biology and conservation of Mediterranean raptors*, 1994. Monografía No. 4. SEO-BirdLife, Madrid, Spain.

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LETTERS

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THE LESSER KESTREL (*FALCO NAUMANNI*) AT DANA NATURE RESERVE, JORDAN

The Lesser Kestrel (*Falco naumanni*) is classified as “Vulnerable” and is a species that has declined dramatically in its western Palearctic breeding range in recent years (N.J. Collar et al. 1994, *Birds to watch 2: the world checklist of threatened birds*, Birdlife Internat., Cambridge, U.K.). Throughout its distribution, the major threat to the Lesser Kestrel is intensive agriculture (i.e., biocides, deep mechanized ploughing, monoculture, elimination of fencelines), which has drastically reduced the supply of large insects, the major food of the species (S. Parr et al. 1995, *Biol. Conserv.* 72:45–53). The Lesser Kestrel has a Palearctic distribution from Iberia to Mongolia and south to the Levant and North Africa (G.M. Tucker and M.F. Heath 1994, *Birds in Europe: their conservation status*, Birdlife Conservation, Series 3, Birdlife Internat., Cambridge, U.K.). In most of Jordan, the species is considered an uncommon visitor and a local breeder in the Syrio-African Rift Valley (I.J. Andrews 1995, *The birds of the Hashemite Kingdom of Jordan*, I.J. Andrews Publ., Musselburgh, U.K.). Five pairs were confirmed to breed in Jordan in the Dana Nature Reserve (DNR; M.I. Evans 1994, *Important bird areas in the Middle East*, Birdlife Conservation, Series 2, Birdlife Internat., Cambridge, U.K.).

To provide baseline data for future monitoring and protection of the nest sites, we conducted a survey at the Dana Nature Reserve (30°37'N, 35°32'E, 15 000 ha in size) from 19–26 April 1997. We censused the breeding population and mapped foraging and breeding sites. We conducted our survey during the peak of the breeding season to locate nest sites to determine colony and breeding population size. The DNR is located in a major gorge flowing from the Sharrah Mountains down to the rift valley floor at sea level (M.I. Evans 1994, *Important bird areas in the Middle East*, Birdlife Conservation Ser. 2, Birdlife International, Cambridge, U.K.). The cliffs at the head of the wadi are of Nubian sandstone. There is oak (*Quercus* spp.) woodland on the steeper slopes, mixed with Jerusalem pine (*Pinus halepensis*), Atlantic pistachio (*Pistacia atlantica*) and extensive areas of herbs and scrub. Steppe-like sage (*Artemisia* spp.) dominates the gentler slopes and the plateaus.

Pairs normally breed in colonies and forage <1 km of the colony (N.P. Williams and M. Yazar 1995, *Biol. Conserv.* 72:45–53). In the past, pairs nested on the highest cliffs and foraged in the adjacent grasslands and cultivated areas on the plateau to the east (D.I.M. Wallace 1984, *Sandgrouse* 6:24–47). We censused Lesser Kestrels at the site by conducting a systematic search of the area by car and on foot for six days during 19–26 April 1997 when reproductive activity should have commenced. We drove on dirt tracks through the grasslands and agricultural areas to locate foraging birds, which congregate at favored spots, where they hover or perch conspicuously. Areas inaccessible by car were censused on foot. The proximity of the foraging areas to nest areas allowed us to follow foraging individuals to nest sites visually. In addition, nests were located by scanning all suitable habitats (i.e., cliffs and old buildings). Lesser Kestrels vocalize frequently during the breeding season and are very conspicuous; this is especially true of the males which have a distinctive, species-specific call that is often given when they approach the colony (J. Boulos, R. Yosef pers. obs.). After locating nest sites and their associated foraging areas, we counted numbers of birds present during several visits. Nest sites were marked on 1:50 000 topographic maps. We used the maximum count for each site to estimate the total population. To avoid inflating our estimates, we counted only those individuals that flew to a nest site with a full crop or food items. Other Lesser Kestrels we observed were considered late migrants or transients. We further assumed that all birds at a colony belonged to that colony only and did not nest at a neighboring colony.

We estimated that 24–28 pairs of Lesser Kestrels bred in the DNR during the 1997 breeding season. They were distributed over five locations: one pair at the Tourist Campsite, a colony of two pairs at Shagg el Kelba, four pairs at Dana Sandstone, six pairs at the Dana Village Cliffs overlooking the village, and 11 pairs at Umed Dims in Wadi Nuwatif. Although we were unable to locate any nest sites outside the reserve boundaries, most of the Lesser Kestrels foraged outside the nature reserve.

All nests were located in natural cliff crevices. Most pairs nested at an average height of 250 m in a very narrow stratum of the white Disi Sandstone that is particularly rich in crevices. Nests were all within the semiarid Mediterranean habitat and faced southeast (Tourist Campsite), east (Shagg el Kelba), south (Dana Sandstone and Umed Dims), and west (Dana Village Cliffs).

The kestrels foraged in the flatter, upper elevations (1150–1600 m) of the Mediterranean Zone and at its interface with the Irano-Turanian zone of the eastern desert fringes. Most of the birds foraged to the east of the cliffs in cultivated fields (mostly wheat; *Triticum* spp.) that had patches of wild grasses and sage. Birds used the prevailing

westerly winds to loft themselves up the Rift Valley slopes from the breeding cliffs to the foraging areas with apparently little effort. The return journey downhill was accomplished by a sharp-angled glide. In this energetically efficient manner, we observed them foraging as far as 3 km away from their nest sites. However, the majority remained within 1 km of their nest sites.

We observed kestrels foraging within DNR only in the open, grassy patches amongst juniper woodlands, and mostly during strong, hot easterly winds (khamsins), which appeared to make flight difficult to and from cultivated fields. We assumed that flying into the easterly winds was energetically more expensive and less profitable in terms of finding prey because we noticed a marked (but unquantified) reduction in the density of calling cicadas (*Cicadoidea* spp.; a major prey item) on the plateaus during the khamsins. In parallel, there was no change in the level of activity of the kestrels during different wind regimes in the sheltered parklands that were below and to the west of the scarp-edge.

The breeding population of Lesser Kestrel in DNR is the only confirmed breeding colony in Jordan (e.g., M.I. Evans 1994, Important bird areas in the Middle East, Birdlife Conservation, Series 2, Birdlife Internat., Cambridge, U. K.). The earliest estimate of the size of this colony was 15–20 pairs between Dana village and the slopes of Barra in late April 1963 (D.I.M. Wallace 1984, *Sandgrouse* 6:24–47) which was very close to our estimate of 24–28 pairs suggesting that the population size is little different from 34 years ago.

Regular censuses are necessary to monitor population fluctuations. The population of Lesser Kestrels at DNR is one of the southernmost in the world and as such is an excellent subject for study of this phenomenon because population fluctuations are most obvious at the extremes of a species' range (R. Nathan et al. 1996, *Israel J. Zool.* 42. 361–375; I. Newton 1998, Population limitation in birds, Academic Press, London, U.K.).

We consider the Lesser Kestrel population at DNR to be extremely vulnerable to the influences of agricultural practices because most of their foraging areas lie outside the reserve. At present the Lesser Kestrel population has a chance to maintain itself because the current cultivation practices in the foraging areas appear to not be intensive, and are located in low-quality agricultural land (shallow, stony calcareous soil). Thus, conservation managers should encourage farmers to maintain low-intensity agricultural practices or they should try to acquire these areas for inclusion in the reserve. It is also imperative to determine the true breeding population in the deserts to the south and east of DNR in order to establish the true breeding population of Lesser Kestrels in the Hashemite Kingdom of Jordan.—**Reuven Yosef, International Birding and Research Center in Eilat, P.O. Box 774, Eilat 88000, Israel, Jacklene Boulos and Omar Tubbeshat¹, Arava Institute for Environmental Studies, D. N. Cheve, Eilat 88840, Israel.**

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BROWN BEAR (*URSUS ARCTOS*) FEEDS ON STELLER'S SEA EAGLE (*HALIAEETUS PELAGICUS*) NESTLING

On 21 July 1997 at about 1900 H, while conducting a survey of Steller's Sea Eagles (*Haliaeetus pelagicus*) along the coast and rivers of the North Okhotsk Sea (Magadan and Okhotsk districts), we witnessed a 3–6-yr-old brown bear (*Ursus arctos*) in the nest of Steller's Sea Eagle feeding upon the remains of an eagle nestling, approximately 8-wk-old. The nest was located atop a rocky pinnacle approximately 9 m in height which was accessible by land only during low tide. From a boat, we observed the bear feeding for about 10 min and were able to approach to within about 25 m, at which time the bear departed. We inspected the nest and found the legs and feathers of one Steller's Sea Eagle nestling and the jaw of a wolf fish (*Anarchalis orientalis*). The nestling remains were fresh and no *rigor mortis* was evident in the tarsometatarsus or phalanges, leading us to believe that the eaglet had been killed by the bear.

Although this is the first time during 6 yr of study that we witnessed a bear feeding on an eaglet, we have seen other indications that bear predation on Steller's Sea Eagle nestlings does occur. In checking 219 nests since 1984, we strongly suspected bear predation of eaglets in four other instances, based on earlier observations of well-grown nestlings, claw-marks high on trees and nest condition.

We regularly found signs of bears near tree and cliff nests and have found the remains of eaglets which apparently fledged, perhaps prematurely, and were subsequently eaten. The areas immediately around many nests in the North

¹ Present address: El Shiya Street, Irbid 1476, Jordan.

Okhotsk sea were crisscrossed by bear trails, and bears probably fed on prey remains which fell from nests. On a number of eagle nest trees, bear claw marks were noted above the height bears could reach from the ground.

Other observers have seen evidence of Steller's Sea Eagle nest depredation by bears. In 1985 on the Yana River, a bear climbed a tree, made a hole in the middle of the nest and took one nestling (V. Pravosudov pers. comm.). Lobkov and Zueva (1983, pages 30–33 in V.M. Galushin [ED.], Ecology of birds of prey, Proc. 1st all-union conference on birds of prey, Moscow, Russia) and Lobkov and Neufeldt (1986, in Proc. Zool. Instit., Acad. Sci., Moscow, Russia) noted bear claw marks on eagle nest trees although they did not state how high above ground level these occurred. They estimated that terrestrial predators may have taken 9–10% of nestlings, although no specific instance of bear predation was documented.

Black bear (*U. americanus*) predation of eaglets has been observed in nests of Bald Eagles (*H. leucocephalus*) in the Yakutat region of southeast Alaska (P. Schempf pers. comm.), British Columbia (McKelvey and Smith 1979, *Murrelet* 60:106–107), and northern California (T. Bills pers. comm.). Black bears are also known to take fledglings of Bald Eagles on the ground (W. Bowerman pers. comm.). Bald Eagle nestlings have been killed in nests by wolverines (*Gulo gulo*, Doyle 1995, *Can. Field-Nat.* 109:115–116) and raccoons (*Procyon lotor*, P. Nye pers. comm.), and lynx (*Felis lynx*) may depredate the nests of White-tailed Sea Eagles (*H. albicilla*) in Norway (T. Nygard pers. comm.). Bears have been known to try to eat nestlings of other birds (e.g., Dixon 1927, *Condor* 29:271–272), but studies of bear diet suggest that birds are rarely eaten (e.g., Holcroft and Herrero 1991, *Can. Field-Nat.* 105:335–345).

Although other carnivores occur in this area, the large size of older nestlings (sometimes >7 kg) probably deters some from eating nestlings. Steller's Sea Eagles do suffer egg predation by stoat (*Mustela erminea*) and sable (*Martes zibellina*) in Kamchatka (Lobkov and Zueva 1983, Lobkov and Neufeldt 1986). Galushin (1983, in N.V. Elisee [ED.], Red data book of Russian Federation, Rosselkhozizdat, Zhivotnie, Russia and 1984, in A.M. Borodin [ED.], Red data book of the USSR, rare and endangered species of animals and plants, 2nd Ed., Vol. 1, animals, Lesnaya Promyshlennost, Moscow, Russia) mentioned mustelid predation but did not say if it was on nestlings.

The nests of *Haliaeetus* eagles are generally very large and often inaccessible. In much of its range, Steller's Sea Eagle nests are often on high, vertical cliffs or in the tops of tall (sometimes dead) trees. The nest size and placement often contributes to its inaccessibility and probably reduces predation by ground predators, like wolves (*Canis lupus*). We do not think that predation by bears or any other predator causes a large reduction in the number of Steller's Sea Eagle fledglings produced each year in the Magadan region. Prey availability and human disturbance are probably more important factors.

Lobkov and Zueva (1983) have suggested that the activities of researchers may attract predators to Steller's Sea Eagle nests. This link between the presence of humans and nest predation has been established in other species (Grier and Fyfe 1987, pages 173–182 in B.A. Giron Pendleton, B.A. Millsap, K.W. Cline and D.M. Bird [EDS.], Raptor management techniques manual, Natl. Wildl. Fed., Washington, DC U.S.A.). It is unlikely that the predation we observed was linked to human activity near the nest because the nest site was very remote and had not been visited by us before in the season.—**M.J. McGrady, Raptor Research Center, Boise State University, Boise, ID 83725 U.S.A., E. Potapov, P.O. Box 239, St. Petersburg 196105, Russia and I. Utekhina, Magadan State Reserve, Portovaya 9, Magadan 685014, Russia.**

OBSERVATION OF A DOUBLE-TOOTHED KITE (*HARPAGUS BIDENTATUS*) HAWKING BATS

The Double-toothed Kite (*Harpagus bidentatus*) inhabits neotropical forests from southern Mexico to southeastern Brazil and eastern Bolivia (Brown and Amadon 1968, Eagles, hawks, and falcons of the world, McGraw-Hill, New York, NY U.S.A.; del Hoyo, Elliot and Sargatal 1994, Handbook of the birds of the world, Vol. 2, New world vultures to guineafowl, Lynx Edicions, Barcelona, Spain). It feeds mainly on insects and small reptiles, and sometimes follows monkey troops, preying on insects and other small organisms startled into motion by primates (Boinski and Scott 1988, *Biotropica* 20:136–143; Egler 1991, *Wilson Bull.* 103:510–512; Fontaine 1980, *Auk* 97:94–98; Greenlaw 1967, *Auk* 84:596–597; Terborgh 1983, Five New World primates, Princeton University Press, Princeton, NJ U.S.A.). In Guatemala, M. Schulze (pers. comm.) found that insects comprised 61.6%, lizards 39.1%, and birds, bats, rats and snakes together <1% of the total ($N = 540$) identified prey items of seven pairs of kites during the 1992–96 reproductive

seasons (February–June). In Costa Rica, Boinski and Timm (1985, *Am. J. Primatol.* 9:121–128) reported an observation of a Double-toothed Kite preying on a tent-making bat (*Artibeus* sp.) flushed by a squirrel monkey (*Saimiri oerstedii*). Here, we describe the hunting and successful capture of bats by a solitary adult Double-toothed Kite.

On 29 March 1996, while searching for Orange-breasted Falcons (*Falco deiroleucus*) in a remote area of western Petén, Guatemala, we observed an adult Double-toothed Kite hunting bats emerging from their cliff crevice roosts near the bottom of a large limestone sinkhole. The sinkhole was about 100 m deep by 150 m in diameter, and its bottom was filled with water. At 1728 H, we observed the kite fly from its perch on the cliff about 10 m above the water, upward a short distance at a steep angle, flip backward until upside down, fully extend its legs, seize a flying bat, return to its perch and begin feeding. After eating the bat, the kite made a similar upward flight next to the cliff and perched at a vertical crevice, holding on to the cliff with one foot and bracing itself with its tail as it probed with its other leg into the cleft for several seconds before returning to its perch without prey. At 1802 H, the kite made another upward flight of about 10 m, again flipped backward in a manner identical to that observed previously, but was unsuccessful and returned to its perch. Though the kite still appeared interested, bobbing its head and showing intention movements at times as if to fly, no subsequent hunting attempts were observed when darkness terminated our observations.

To our knowledge, Double-toothed Kites have not been previously reported to capture highly mobile aerial prey on the wing.

ACKNOWLEDGMENTS

We gratefully acknowledge Robert Berry and The Peregrine Fund for financial support for this research, Mark Schulze for sharing data on breeding biology and diet and Danny Harris and Lloyd F. Kiff for critical comments on the manuscript.—**Aaron J. Baker and David F. Whitacre, The Peregrine Fund, 566 W. Flying Hawk Lane, Boise, ID 83709; Oscar A. Aguirre-Barrera and Juventino López Avila, Fondo Peregrino, Parque Nacional Tikal, Petén, Guatemala; and Clayton M. White, 574 WIDB, Department of Zoology, Brigham Young University, Provo, UT 84602.**

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RECORDS OF THE SWAINSON'S HAWK IN THE CAPE REGION, BAJA CALIFORNIA SUR, MEXICO

This is the second record in the last 20 yr of the Swainson's Hawk (*Buteo swainsoni*) in the Cape Region, Baja California Sur, Mexico. Our observations were from the La Paz coastal plain near Ensenada de Aripes. This is a suburban and agricultural area through which we drive daily. Halophytes dominate the coastal plain and the climate is BW (h') hw (x') (INEGI 1994, Carta Estatal, Anexo Cartográfico, Síntesis Geográfica del Estado de Baja California Sur, La Paz, México). In México, the Swainson's Hawk is found in the northern Baja California Peninsula from Sonora to eastern Durango and Coahuila and possibly in northern Nuevo León (Howell and Webb 1995, *The birds of Mexico and Central America*, Oxford Univ. Press, London, U.K.). In the northern Baja California Peninsula, the Swainson's Hawk is considered to be fairly common locally as a transient or summer visitor (Grinnell 1928, *A distributional summation of the ornithology of Lower California*, Cambridge Univ. Press, New York, NY U.S.A.). Its current status is uncertain in the southern peninsula with only one hawk sighted on 31 October 1968 in Cabo San Lucas, Baja California Sur (Wilbur 1987, *Birds of Baja California*, Univ. California Press, Berkeley, CA U.S.A.). Swainson's Hawk habitat includes savanna, grassy plains and farmland with scattered trees and bushes. The Mexican name for Swainson's Hawk is "gavilán chapulinero" or "aguililla de Swainson."

In 1998, we recorded six sightings of a Swainson's Hawk, probably all the same individual, southeast of Ensenada de Aripes, bordering the highway Carretera Transpeninsular in El Centenario (24°06'36"N, 110°25'05"W) and west of La Paz (24°06'27"N, 110°21'31"W). All the sightings were of a solitary individual either flying or perched on power lines and poles. It was an adult, light morph with a conspicuous breastband, with a white throat and belly and dark tail that was lighter at the base with indistinct dark bands. The hawk was first seen on 18 and 20 January and was not seen again until nine months later when we saw it on 31 October, 21 and 23 November, and 1 December.

Other raptors were observed with this Swainson's Hawk. They included Turkey Vultures (*Cathartes aura*), Red-tailed Hawks (*Buteo jamaicensis*), Zone-tailed Hawks (*B. albonotatus*), Crested Caracaras (*Polyborus plancus*) and American Kestrels (*Falco sparverius*). There are also Cooper's Hawks (*Accipiter cooperii*) and Ospreys (*Pandion haliaetus*) in the area (Romero and Rodríguez 1981, *Densidades en las poblaciones, biomasa, hábitos alimenticios y estratificación de*

la avifauna en un ecosistema del desierto sonorense, La Paz, B.C.S., México). The Swainson's Hawk is a migratory species and does not overwinter in the Cape Region. Its occurrence in this area of Mexico in 1998 may have been caused by anomalies associated with El Niño in 1997.—**E. Amador and R. Mendoza-Salgado, Centro de Investigaciones Biológicas del Noroeste, S.C., P.O. Box 128, La Paz Baja California Sur, 23000 México.**

JOURNAL OF RAPTOR RESEARCH

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BY ELISE VERNON SCHMIDT

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